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Rift valley-driven species richness, composition and phenology of Odonata in central Zambia

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Abstract

One hundred and seven species of damselflies and dragonflies were recorded at 66 localities in central Zambia during three expeditions between 2013 and 2017, with 104 species at 62 localities in the main study area, in broad environs of Chingombe. The relatively great richness and composition of the odonate fauna in this small remote area was a consequence of the close proximity of three quite different geomorphological units – the flat bottom of the rift valley, the steep mountainous slopes bordering it, and undulating uplands, with a combination of their climatic and hydrological conditions. An odonatological 'river-continuum' sequence was studied, from the upper and lower reaches of the mountain stream, through submontane streams and rivers down to the large river draining the rift valley. This spatial sequence was characterised by large-scale interpenetration of the odonate assemblages, with more specific fauna of the mountain stream and large river, and rich, but less specific that of submontane watercourses. Fluent replacement of some species with their related counterparts was recorded, i.e. more upland species of closed habitats by species related to semi-open lower-elevated watercourses. The range of species well adapted to temporary waters was rich but differed between the small waters of the tropical savannah bottom of the rift valley and larger and longer existing water bodies in seasonally inundated dambos in more subtropical uplands.

The phenological pattern was generally well-structured due to two distinct peaks, the first in the first phase of the wet season, both in the large river and temporary waters, and the second at the end of the wet season, in the latter. Phenology of odonate assemblages in the temporary waters was based on two consecutive aspects dominated respectively by adults reproductively active in the early–mid season and tenerals emerging at the end of it. At the beginning of the wet season, the reaction of adult odonates to first heavier rains was extremely rapid and even preceded the formation of the seasonal water body. In the large river, the phenological shift towards the early wet season with a low-water phase and favourable habitat conditions was clearly discernible. In turn, the odonate fauna in another low-water phase, at the end of the wet season and before a cool phase of the dry season, was dramatically poor. In the smaller permanent watercourses, phenology of the odonate assemblages during the wet season was generally less patterned, without a dramatic change of generations and with the emergence more dispersed in time, though centred on the first half of the season. As an effect of replacing individuals and the prolonged occurrence of many species, the odonate assemblages, while richer in the first half of the

rainy season, appeared more stable and continuous than those of the temporary waters and the large river.

Key words: Dragonfly, damselfly, Zygoptera, Anisoptera, Afrotropics, odonate assemblages, miombo woodlands.

Introduction

Faunistic records, taxonomy and zoogeography have been major aspects of numerous publications on Afrotropical odonates so far. Species richness has mostly been analysed on the large territorial scale of the African continent (e.g. Clausnitzer et al. 2012) or geographical regions and countries, such as Eastern Africa from Sudan to Zimbabwe (Dijkstra & Clausnitzer 2014), Namibia (Suhling & Martens 2014), Botswana (Kipping 2010), Angola (Kipping et al. 2017) and South Africa with Lesotho and Eswatini (e.g. Pinhey 1951; Tarboton & Tarboton 2019). Publications focused on local species richness and odonate assemblages have been less frequent (e.g. Fraser 1955; Legrand, Couturier 1985; Clausnitzer 1999, 2006; Kipping 2002; Dijkstra 2004, 2007; Seidu et al. 2017; Kipping et al. 2018). Only some of these were syntheses sufficiently extensive to comprehensively show a local picture of the odonate fauna with its habitat-specific traits and seasonal changes.

We organized three expeditions to central Zambia in various phases of the rainy season, in-XII-2013,-IV-2015 and-I-2017. Apart from several localities visited on the way (in and near Kabwe), our studies were intentionally focused on a small remote area combining the bottom of the rift valley (the Luano Valley), its mountain slopes (the Muchinga Escarpment) and the adjacent upland plateau. Focusing our activity in terms of space and extending it widely in time gave us the possibility to study the local fauna in greater depth. The aim of this paper was thus to show local species richness and odonate assemblages in central Zambia, with attention paid to their dynamics and diversity in space and time. The rift valley, which significantly enriches local habitat and climatic conditions in this rather monotonous upland province, was a key factor in this study.

Zoogeographical and taxonomic aspects of the results had already been analysed in two previous papers (Bernard & Daraż 2018; Bernard et al. 2018), where twenty-three species were included, namely those that were especially interesting in this respect, and thus required broader treatment. However, the basic data on these species were repeated in the current paper, as they were necessary to complete the picture of the odonate fauna analysed from a different angle.

Study area and localities

All 66 localities were situated in the Central Province of Zambia and almost all (loc. 1–62) in the main area of study, in the broad environs of Chingombe in the remote part of the Luano district (Fig. 1). Additionally, one locality (loc. 63, Lunsemfwa) was situated between the main study area and Kabwe and three other localities (loc. 64–66) in Kabwe and its environs.

The main study area (Fig. 1) mainly included the picturesque Luano Valley, which is, in fact, the Lukusashi Rift Valley (Fig. 2), located parallel to the Luangwa Rift Valley, but separated from it by a mountain ridge. The study area comprised three different landscape
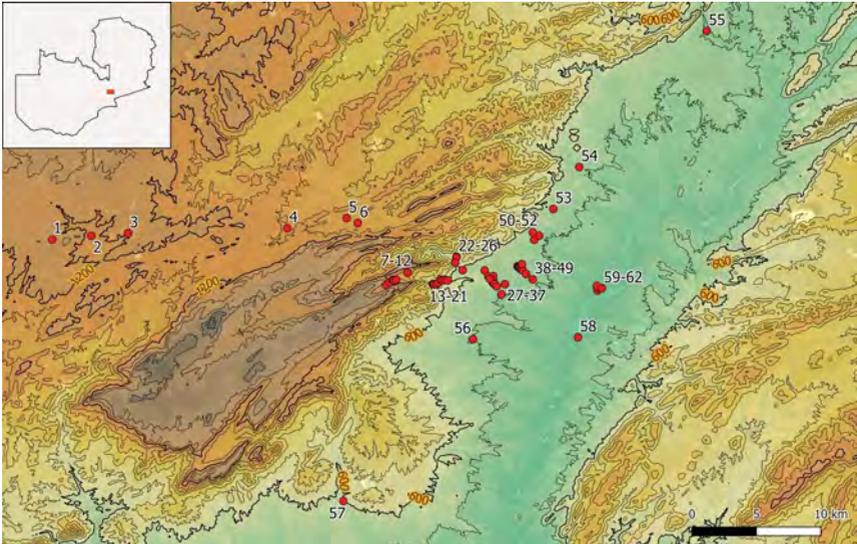
Fig. 1. The study area in central Zambia with the bottom of the Lukusashi Rift Valley (the Luano Valley, roughly below 600 m a.s.l.), the mountains of the Muchinga Escarpment (600–1600 m a.s.l.) bordering it from the east, and the upland plateau (1040–1250 m a.s.l.) situated on the opposite side of the mountains. The numbers of the localities follow the list in the text.

Fig. 2. The Lukusashi Rift Valley (= the Luano Valley), a "window" view from the slopes of the Muchinga Escarpment.

Fig. 3. The flat bottom of the Lukusashi Rift Valley flanked from the west by a mountain ridge separating it from the parallel Luangwa Rift Valley.

Fig. 4. Mountains of the Muchinga Escarpment seen from the bottom of the rift valley.

units (Fig. 1): the bottom of the rift valley (loc. 22 and 26–62), the mountain slopes of the valley, i.e. the Muchinga Escarpment (loc. 7–21 and 23–25) and the adjacent upland plateau (loc. 1–6).

An axis of the rift valley is the Lukusashi River, a medium-size to periodically large watercourse. The bottom of the rift valley (Fig. 3) ranges between 435 and 580–600 m a.s.l. and is flat to gently undulated, relatively hot and overgrown by drier and looser (also due to human exploitation) forms of miombo and mopane woodlands. Two villages and several small settlements stretch along several permanent streams and small rivers bringing water from uplands. The adjacent mountain slopes of the Muchinga Escarpment (Fig. 4) – studied roughly between 590–1200 m a.s.l. but reaching 1400–1600 m – are covered by more natural and moister forms of miombo woodlands. Additionally, mature gallery forest occurs there along permanent, typically mountainous watercourses, often flowing in deep and narrow valleys. On the opposite side, the mountainous Muchinga Escarpment descends and merges fluently into the upland plateau (1040–1250 m a.s.l.) (Fig. 5). The plateau is undulated and abounds in dambos (Figs 6 and 8), i.e. linear, river-like, shallow, open (lacking woodlands) depressions situated between the slopes with miombo woodlands. They are seasonally waterlogged and partly inundated with water during and after the wet season (Goudie 1996).

Fig. 5. The barely passable road to Chingombe through the upland plateau and the mountains of the Muchinga Escarpment (visible in the background).

The climate of the main study area ranges between the tropical savanna climate at the bottom of the rift valley and humid subtropical climate at higher elevations (Beck et al. 2018). In both versions, it is markedly seasonal with two distinct seasons, dry (May–October) and wet (November/December–April). The latter brings c. 800–1100 mm of precipitation (Waldman et al. 2019 and unpublished data from the Chingombe Catholic mission), with the driest zone being the bottom of the rift valley and moister areas in the mountains and plateau.

Fig. 6. Dambo Kabufumu (loc. 1): (A) in the early wet season, still without water above ground level (20-XII-2013), *Lestes amicus, L. dissimulans, L. virgatus, Aciagrion africanum, Africallagma fractum, A. pallidulum, Ceriagrion banditum, Anax ephippiger, A. tristis;* **(B) in the peak of the wet season (31-I-2017),** *Lestes amicus, L. dissimulans, L. virgatus, Ceriagrion banditum, C. glabrum, Pseudagrion hamoni, Acisoma inflatum, Crocothemis erythraea, Diplacodes deminuta, D. lefebvrii, D. luminans, Orthetrum brachiale, Tramea limbata, Trithemis arteriosa.*

Fig. 7. The Busanga Stream, a calm section at the beginning of the wet season (loc. 2, 5-XII-2013). *Lestes plagiatus, Anax speratus, Nesciothemis farinosa, Trithemis stictica***.**

Fig. 8. Dambo Kabasa at the end of the wet season (loc. 3, 30-IV-2015). *Lestes amicus, L. dissimulans, L. plagiatus, L. virgatus, Aciagrion africanum, Africallagma fractum***,** *Agriocnemis exilis, Ceriagrion banditum, C. glabrum, Pseudagrion hamoni, Anax imperator, Aethiothemis bequaerti, A. solitaria, Crocothemis erythraea, Diplacodes luminans, Orthetrum brachiale, Tholymis tillarga, Tramea limbata***.**

In the list, the following information is given for each locality: a) its number, b) its location described geographically and situated in a landscape unit in relation to altitude, and c) a brief description with features necessary to draw odonate habitats. The representative examples of habitats are illustrated on photographs. Their captions include lists of species recorded at the localities in the specified dates; some captions comprise several visits.

1. Dambo Kabufumu, 34.5 km WNW of the Chingombe Catholic mission, by the road to Old Mkushi; 14°23.31' S, 29°38.96' E, 1,230 m a.s.l. – the plateau; a large (90×30 m) temporary pool in the dambo (Fig. 6). With crystal water up to 1 m deep and with abundant *Cyperus* sp., grasses and a large patch of *Persicaria senegalensis* f. *albotomentosa*.

2. The Busanga Stream, 31.4 km WNW of the Chingombe Catholic mission, at the road to Old Mkushi; 14°23.14' S, 29°40.64' E, 1,170 m a.s.l. – the plateau. Permanent, narrow with broader calm pools (0.3–2.5 m wide) (Fig. 7). Abundant vegetation in the stream pool: emergent (*Phragmites mauritianus*, *Schoenoplectus* sp.) and nymphaeids (*Nymphaea caerulea*). Open and partly shaded by overhanging bushes.

3. Dambo Kabasa, 28.5 km WNW of the Chingombe Catholic mission, by the road to Old Mkushi; 14°23.04' S, 29°42.23' E, 1,200 m a.s.l. – the plateau; a large (50x45 m) pool in the dambo (Fig. 8), generally temporary, but in the wettest years (as in 2015 and preceding years) possibly semi-permanent. With rich and abundant vegetation: emergent grassy and *Schoenoplectus*-like along shores, nymphaeids *Nymphaea caerulea* on the water table and submerged *Ottelia ulvifolia*.

4. The Ndauni Stream, upper reaches, 16.5 km WNW of the Chingombe Catholic mission, at the road to Old Mkushi; 14°22.82' S, 29°49.11' E, 1,085 m a.s.l. – the plateau. Permanent, narrow (0.5–1.5 m), with stronger-current and calmer sections. Sandy bottom deposits with various amounts of detritus and stones and boulders. Shaded with clearings.

5. The Chilimulilo Stream, a tributary of the Fiperere Stream, 12.5 km NW of the Chingombe Catholic mission, at the road to Old Mkushi; 14°22.39' S, 29°51.68' E, 1,045 m a.s.l. – the plateau. Permanent, narrow (1–2.5 m) with deeper sections and shallower rapids. Sandy, sandy-gravelly and stony bottom deposits. Mostly shaded with some clearings.

6. The Fiperere Stream, upper reaches, 11.5 km NW of the Chingombe Catholic mission, at the road to Old Mkushi; 14°22.60' S, 29°52.17' E, 1,040 m a.s.l. – the plateau. Permanent, narrow. Sandy, sandy-gravelly and sandy-stony bottom deposits with many boulders. Mostly shaded with some clearings.

7. The Mikwa Stream, uppermost reaches, just below a source, 8.3 km W of the Chingombe Catholic mission; 14°25.27' S, 29°53.39' E (to 100 m upstream and downstream), 1,180 m a.s.l. – the mountains. Permanent, narrow (0.5–2 m), with heterogeneous morphology (boulders, cascades, strong-current sections and calm deeper stream pools) and correspondingly diverse bottom deposits from gravelly and sandy up to muddy with a thick layer of detritus. Locally with side seepages. Deeply shaded by a gallery forest, with small clearings (Fig. 9, 10).

8. The Mikwa Stream, upper reaches, 8.0 km W of the Chingombe Catholic mission; 14°25.15' S, 29°53.51' E, 1,160 m a.s.l. – the mountains. For the habitat description, see [7.].

Fig. 9. The Mikwa Stream, upper reaches, at the end of the wet season (loc. 7, 25-IV-2015). *Chlorocypha consueta, Elattoneura cellularis, Pseudagrion hageni, P. kersteni, Crocothemis sanguinolenta, Orthetrum julia*.
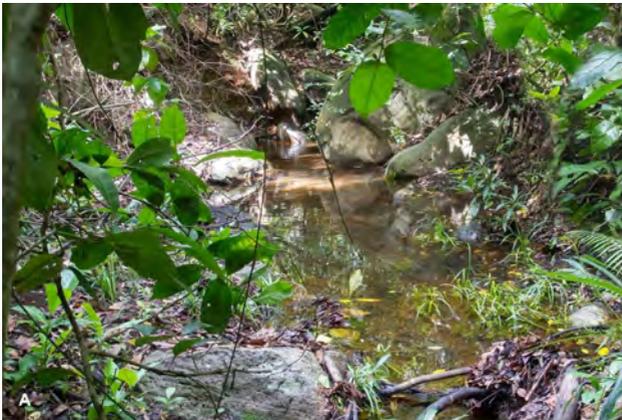
Fig. 10. The Mikwa Stream, upper reaches, during the peak of the wet season (loc. 7, 26–28 -I-2017): (A) a stream micropool closed by a natural dam, with (B) the bottom covered with a thick layer of leaves and soft detritus. *Chlorocypha consueta, Allocnemis marshalli, Elattoneura cellularis, Pseudagrion hageni, Heliaeschna fuliginosa, Anax speratus, Phyllomacromia monoceros, Notiothemis jonesi, Orthetrum julia* (on slopes above, also *Pseudagrion spernatum*).

9. The Mikwa Stream, upper reaches, 7.7 km W of the Chingombe Catholic mission; 14°25.04' S, 29°53.67' E, 1,120 m a.s.l. – the mountains. For the habitat description, see [7.]. Additionally, the main stream is fed by a smaller watercourse and side trickles.

10. A source of a small tributary of the Mikwa Stream, 7.7 km W of the Chingombe Catholic mission;14°25.07' S, 29°53.72' E, 1,130 m a.s.l. – the mountains. Small (1.5x2.5 m), shallow (1–7 cm), fairly densely overgrown by various Cyperaceae. Situated in an open, grassy area with seepages.

11. A small tributary of the Mikwa Stream, 7.5 W of the Chingombe Catholic mission; 14°25.03' S, 29°53.81' E, 1,110 m a.s.l. – the mountains. Narrow (0.3–0.6 m, exceptionally 1.5 m) headwater mountain stream: steep, with cascades and shelves, calmer and faster sections, sandy bottom, locally with detritus. Shaded with clearings. Additionally, a small (1.8 m^2) pool, situated next to the stream and temporarily fed by a trickle; with clear water (30–40 cm deep) and a lot of old leaves (Fig. 11).

Fig. 11. Headwater mountain stream (a tributary of the Mikwa Stream) with an adjacent small pool, during the peak of the wet season (loc. 11, 26-I-2017). *Chlorocypha consueta, Allocnemis marshalli, Notiothemis jonesi, Orthetrum julia.*

12. The Mikwa Stream, upper reaches, 6.7 km WNW of the Chingombe Catholic mission; 14°24.74' S, 29°54.30' E, 1,060 m a.s.l. – the mountains. Permanent, narrow (1–2 m). Sandy bottom deposits, locally with stones and boulders. Shaded with many small clearings.

13. Seepage feeding a tributary of the Mikwa Stream, 4.6 km W of the Chingombe Catholic mission; 14°25.22' S, 29°55.40' E, 680 m a.s.l. – the mountains. Small (7 m^2), flowing from under a rock, with warm water and loose vegetation. Partly sunny.

14. The Mikwa Stream, lower reaches below the waterfall, mouth of a tributary 4.6 km W of the Chingombe Catholic mission; 14°25.22' S, 29°55.41' E, 680 m a.s.l. – the mountains. The main stream is a few metres wide, permanent, strong-current, with many boulders and riffles. The tributary stream is semi-permanent, highly astatic (hardly present to strong), with a chain of small cascades and rocky and sandy-stony (with detritus) bottom. Additionally, rocky seepages and a deep pool fed by a side branch of the main stream. Partly sunny.

15. The Mikwa Stream, lower reaches below the waterfall, 4.6 km W of the Chingombe Catholic mission; 14°25.23' S, 29°55.45' E, 670 m a.s.l. – the mountains. Permanent, a few metres wide, with a gravelly-stony bottom, boulders and riffles. Shaded by a gallery forest (Fig. 12).

16. The Mikwa Stream, lower reaches, 4.4 km W of the Chingombe Catholic mission; 14°25.25' S, 29°55.56' E (to 200 m upstream and 400 m downstream), 640–660 m a.s.l. – the mountains. Permanent, 3–6 m wide, with a sandy, gravelly and gravelly-stony bottom, boulders and riffles (Fig. 12). Shaded by a gallery forest with clearings, on a short section semi-open with *Cyperus involucratus*.

Fig. 12. The Mikwa Stream, mountainous lower reaches (loc. 15–16, 7-XII-2013, 19-IV-2015, 20-I-2017). *Phaon iridipennis, Chlorocypha consueta, Platycypha caligata, Elattoneura cellularis, Pseudagrion hageni, P. kersteni, Notogomphus cf. zernyi, Orthetrum julia, Trithemis aconita, Zygonyx natalensis, Z. torridus.*

17. A pool 'hanging' in an earth-slip on the slope of the Mikwa Stream valley, 10 m above the stream, 4.2 km W of the Chingombe Catholic mission; 14°25.17' S, 29°55.63' E, 640 m a.s.l. – the mountains. Small (4–5 m²), deep (>1 m). Water not transparent, warm, fed by a warm-water seepage trickle. Shaded with clearings (Fig. 13).

Fig. 13. A pool 'hanging' in an earth-slip on the slope of the Mikwa Stream valley during the peak of the wet season (loc. 17, 20-I-2017). *Notiothemis jonesi*.

18. The Mikwa Stream, lower reaches, 4.1 km W of the Chingombe Catholic mission; 14°25.04' S, 29°55.73' E, 630 m a.s.l. – the mountains. Undercutting steep cliff, permanent, 2.5–3.5 m wide. Locally calmer, 30–40 cm deep, with muddy bottom deposits and abundant detritus, and locally stronger, a few centimetres deep, with a sandier bottom and a boulder cascade. Partly overgrown with *Cyperus involucratus* along shores. Open, sunny.

19. The Mikwa Stream, lower reaches, 3.9 km W of the Chingombe Catholic mission; 14°25.07' S, 29°55.82' E, 620 m a.s.l. – the mountains. Permanent, 3–5 m wide, with a sandy-gravelly and gravelly-stony bottom (locally covered with detritus), boulders and small riffles. Uncommon *Cyperus involucratus* along shores. Shaded by a high gallery forest with clearings. At the lower border, with an open area, calmer, sunny and totally overgrown with *C. involucratus* and *Phragmites mauritianus*.

20. Rocky pools near the Mikwa Stream, 3.7 km W of the Chingombe Catholic mission; 14°25.05' S, 29°55.94' E, 610 m a.s.l. – the mountains. Small (the largest 1.7x1.2 m), mostly temporary, but the largest possibly semi-permanent as fed by a seepage trickle. Rocky and muddy bottom with old leaves. Partly open, sunny, but the largest shaded with clearings.

21. The Mikwa Stream, lower reaches, 3.5 km W of the Chingombe Catholic mission; 14°25.05' S, 29°56.04' E, 610 m a.s.l. – the mountains. Permanent, narrow (2.5–3 m), shallow (mostly 10–20 cm), with a sandy-gravelly-stony bottom. Open and semi-open, sunny, with abundant vegetation (*Cyperus involucratus*, *Phragmites mauritianus*), even overgrowing the whole streambed. Locally shaded with clearings, without vegetation, but with boulders and riffles.

22. The Mikwa Stream near the mouth to the Chingombe River, 2.5 km NW of the Chingombe Catholic mission; 14°24.64' S, 29°56.68' E, 560 m a.s.l. – the bottom of the rift valley. Permanent, a few metres wide, partly overgrown with vegetation, sunny.

23. The Chingombe River, the 2nd river ford on a track from Chingombe, 3.5 km NW of the Chingombe Catholic mission; 14°24.05' S, 29°56.43' E, 595 m a.s.l. – the mountains. Permanent, 8–9 m wide. In the main branch, a strong current, riffles and boulders; in the narrow side branch, much calmer, relatively deep (up to 0.7 m) and muddy, or shallower with a sandy-gravelly-stony bottom with detritus. Shaded with clearings to semi-open.

24. Woodland clearing adjacent to the Chingombe River, 3.45 km NW of the Chingombe Catholic mission; 14°24.09' S, 29°56.41' E, 600 m a.s.l. – the mountains; open and semi-open, sunny, moist, overgrown with herbaceous vegetation.

25. The Chingombe River, the 1st river ford on a track from Chingombe, 3.3 km NW of the Chingombe Catholic mission; 14°24.30' S, 29°56.37' E, 590 m a.s.l. – the mountains. Situated in a gorge, permanent, 7–10 m wide, with a very strong current, stony bottom and boulders. Shaded with clearings, locally sunny (Fig. 14).
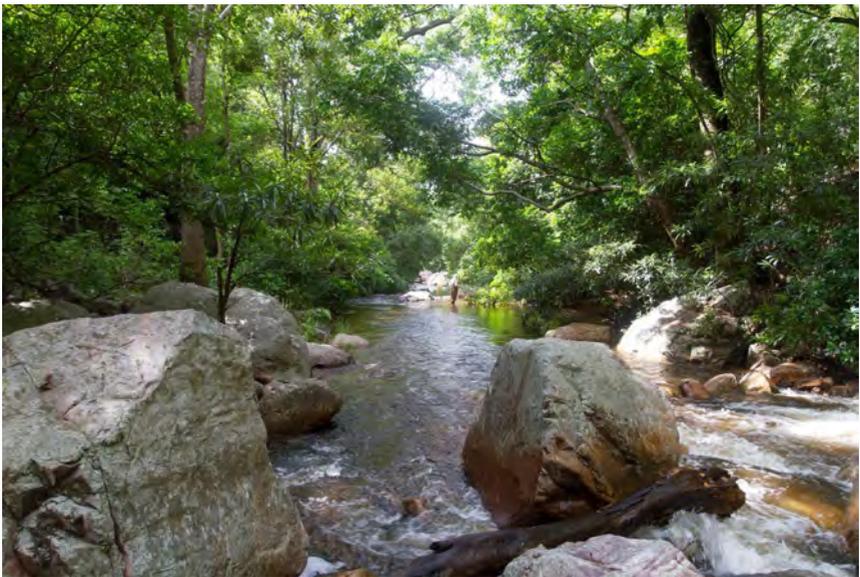
Fig. 14. The Chingombe River in a mountainous gorge during the peak of the wet season (loc. 25, 23-I-2017). *Phaon iridipennis, Chlorocypha consueta, Platycypha caligata, Elattoneura cellularis, Zygonyx natalensis, Z. torridus*.

26. The Chingombe River at the mouth of the Mikwa Stream, 2.55 km NW of the Chingombe Catholic mission; 14°24.63' S, 29°56.69' E, 560 m a.s.l. – the bottom of the rift valley. Permanent, a few metres wide, with a strong current and vegetation along shores, sunny.

27. The Chingombe River, 1.15 km NNW of the Chingombe Catholic mission; 14°24.65' S, 29°57.64' E, 530 m a.s.l. – the bottom of the rift valley. Permanent, 4–5 metres wide, to 0.8 m deep, with a strong current, gravelly (with some detritus) or stony bottom with boulders. *Phragmites mauritianus* along shores. Open, sunny.

28. The Chingombe River, 0.5 km N of the Chingombe Catholic mission; 14°24.88' S, 29°58.01' E, 520 m a.s.l. – the bottom of the rift valley. Fork of the river and a canal going to a small power station. Permanent, 2.5–6 m wide, (0.1)0.4–0.6 m deep. Highly diversified: from deep and calm meandering sections with a sandy and gravelly bottom to shallow and strong-current places with a stony bottom and riffles. 'Walls' of *Phragmites mauritianus* along shores and overhanging the water. Generally open and sunny, but locally (especially along shores) shaded by bushes and high *Phragmites* (Fig. 15).

Fig. 15. The Chingombe River at the bottom of the rift valley in a stony (A) and sandy (B) version in the early and late wet season, respectively (loc. 28,-XII-2013 and-IV-2015). *Platycypha caligata, Phaon iridipennis, Elattoneura glauca, Pseudagrion acaciae, P. gamblesi, P. kersteni, P. sublacteum, Anax speratus, Gomphidia quarrei, Lestinogomphus angustus, Olpogastra lugubris, Orthetrum chrysostigma, Trithemis pluvialis, Zygonoides fuelleborni, Zygonyx torridus.*

29. The Chingombe River, a road ford 0.95 ESE of the Chingombe Catholic mission; 14°25.22' S, 29°58.51' E, 510 m a.s.l. – the bottom of the rift valley. Permanent, highly diversified: from an open, broader (to 10–20 m) and calm fragment to a narrow and strong-current section; additionally a side trickle and some flooded places among grasses. Locally *Phragmites mauritianus* along shores. Sunny.

30. Chingombe Catholic mission, near a small power station; 14°25.07' S, 29°58.02' E (in the range of 100 m), 520 m a.s.l. – the bottom of the rift valley. Mosaic of open areas with single trees and loose banana plantations, mango woodlands and a dense wet forest patch. With a permanent concrete canal of the power station, a temporary shaded canal operating only during high water phases in the rainy season and a small pool in the forest.

31. Chingombe, the Catholic mission; 14°25.17' S, 29°57.99' E, 530 m a.s.l. – the bottom of the rift valley. Open areas overgrown with herbaceous vegetation and some trees/tree groups; regularly used by many foraging dragonflies originating from other localities, e.g. from loc. 33.

32. Chingombe, the Catholic mission, school; 14°25.21' S, 29°58.02' E, 520 m a.s.l. – the bottom of the rift valley. Open and semi-open areas, overgrown with dense herbaceous vegetation, some trees and bushes; regularly used by foraging dragonflies originating from other localities, e.g. from loc. 33. Also, seepages and temporary concrete and stony puddles (to 1.5 m^2 large and 1–2 cm deep) around the school walls (collecting roof rainwater).

33. Chingombe, a canal below the Catholic mission; 14°25.23' S, 29°58.07' E, 515 m a.s.l. – the bottom of the rift valley. Bringing water from the power station, but here already looking like a natural stream, 2.5–3 m wide, (0.1)0.3–0.5 m deep, with a sandy and gravelly bottom and a strong current. Both open and shaded by trees, bushes and 'walls' of high herbaceous vegetation with *Phragmites mauritianus*. Locally grassy patches in shallower water.

34. A pool in the fields, 0.4 km SE of the Chingombe Catholic mission; 14°25.32' S, 29°58.16' E, 510 m a.s.l. – the bottom of the rift valley. Small, bordered and partly over-grown with dense herbaceous and bushy vegetation.

35. A complex of a temporary pond, a narrow temporary stream feeding it and adjacent temporarily flooded grasslands, 0.6 km NNW of the Chingombe Catholic mission, near a cemetery; 14°24.90' S, 29°57.80' E, 530 m a.s.l., the bottom of the rift valley. Small pond (10x12 m), shallow in the beginning of the rainy season and even 1 m deep at the end of it; in 2013 partly and in 2015 totally densely overgrown by *Phragmites mauritianus* and other grassy and *Cyperus*-like vegetation (Fig. 16).

36. A temporary streamlet, 0.35 km NNW of the Chingombe Catholic mission, near a ceme-tery; 14°25.00' S, 29°57.86' E, 525 m a.s.l., the bottom of the rift valley. Flowing in the rainy season between dense herbaceous vegetation and bushes, both sunny and shaded, narrow (0.5–1 m), locally with some stones in open places.

37. Peter Kaimfa's fishponds in Chingombe, 1.1 km SE of the Chingombe Catholic mission; 14°25.66' S, 29°58.36' E, 505 m a.s.l., the bottom of the rift valley. A chain of several small ponds, fed by a permanent streamlet (0.2-0.3 m wide in high grass); during the study, only one pond (8x15 m) was used for aquaculture, deep, with water table partly overgrown with low water vegetation, other ponds only with trickles and rain-water in the deepest points (to 0.5 m deep, present during the rainy season), over-grown with rich, locally abundant and high herbaceous vegetation. Sunny.

Fig. 16. A temporary pond in Chingombe in the early wet season (loc. 35,-XII-2013). *Lestes plagiatus, Ceriagrion banditum, C. glabrum, Pseudagrion commoniae, Anax tristis, Diplacodes luminans, Orthetrum brachiale, Palpopleura portia, Tramea basilaris, Trithemis arteriosa* **(in the late wet season in-IV-2015, also** *Agriocnemis gratiosa* **and** *Africallagma fractum***).**

38. A pool on the Mulembwe temporary stream, 2.3 km NE of the Chingombe Catholic mission; 14°24.45' S, 29°59.06' E, 530 m a.s.l. – the bottom of the rift valley. Small and shallow (to >0.5 m), temporary, but relatively persistent in this category or possibly even semi-permanent in wettest years. Overgrown with abundant *Schoenoplectiella lateriflora* (in Bernard & Daraż 2018, erroneously given *lacustris*), but in 2017, after the drought of 2016, only by grassy vegetation. Partly shaded, surrounded by miombo woodlands and grassy areas (Fig. 17).

39. The Mulembwe (=Milembwe) Stream, upper reaches above the road, 2.35 km NE of the Chingombe Catholic mission; 14°24.47' S, 29°59.09' E, 530 m a.s.l. – the bottom of the rift valley. Temporary (existing in the rainy season), 0.4–1 m wide (locally with small pools or shallowly flooded), several to 15 cm deep, flowing between grass, without vegetation to totally overgrown, locally with stones. Sunny, surrounded by grassy areas and miombo woodlands (Fig. 19a).

40. A pool on the Mulembwe (temporary) stream above the road, 2.35 km NE of the Chingombe Catholic mission; 14°24.50' S, 29°59.10' E, 525 m a.s.l. – the bottom of the rift valley. Small, astatic, possibly semi-permanent in wettest years, but temporary in most years; 0.2–0.5 m deep, muddy, partly overgrown with rich vegetation in the more permanent phase (emergent *Schoenoplectiella lateriflora*, nymphaeids *Nymphaea caerulea*, and submerged *Myriophyllum* sp.). Generally sunny, but partly shaded by overhanging bushes. Surrounded by miombo woodlands and grassy areas (Fig. 18).

Fig. 17. A pool in the upper reaches of the temporary Mulembwe Stream (loc. 38): (A) in the late wet season (April 2015) before the drought of 2016, and (B) in the mid-rainy season (January 2017) after the drought of 2016 (Bernard et al. 2018). *Lestes ictericus, Agriocnemis exilis, Ceriagrion glabrum, C. mourae, C. suave, Pseudagrion commoniae, P. hamoni, Anax ephippiger, A. tristis, Crocothemis erythraea, Diplacodes deminuta, D. luminans, Orthetrum brachiale, Palpopleura deceptor, P. lucia, Pantala flavescens, Tramea basilaris, Trithemis arteriosa.*

Fig. 18. A pool in the upper reaches of the temporary Mulembwe Stream (loc. 40) in the late wet season (April 2015). *Crocothemis erythraea, Diplacodes luminans, Palpopleura lucia* **(during the peak of the wet season in late January, also** *Orthetrum brachiale, Pantala flavescens, Palpopleura deceptor,* **and** *Tramea basilaris***).**

41. Road puddles at the Mulembwe Stream, 2.35 km NE of the Chingombe Catholic mission; 14°24.52' S, 29°59.13' E, 525 m a.s.l. – the bottom of the rift valley. Two large puddles (up to 20 m long, several metres wide and more than a dozen cm deep), temporary but existing for months in the rainy season; mostly bare, devoid of vegetation, but also including flooded roadsides with low vegetation. Sunny.

42. The Mulembwe Stream at the road, 2.35 km NE of the Chingombe Catholic mission; 14°24.52' S, 29°59.14' E, 525 m a.s.l. – the bottom of the rift valley. Temporary (existing in the rainy season), very shallow, in a twenty-metre-long section freshly cleaned during the renovation of the road, thus completely bare.

43. The Mulembwe Stream, below the road; 2.4 km NE of the Chingombe Catholic mission; 14°24.55' S, 29°59.18' E, 520 m a.s.l. – the bottom of the rift valley. Temporary (existing in the rainy season), 0.4–1 m wide, several to 15 cm deep, flowing between grass and stones, locally more open and stony. Sunny, surrounded by grassy areas and miombo woodlands.

44. A pool on the Mulembwe temporary stream, 0.2. km below the road, 2.4 km NE of the Chingombe Catholic mission; 14°24.59' S, 29°59.20' E, 520 m a.s.l. — the bottom of the rift valley. Temporary, small (120 m^2), shallow (10–30 cm), with grassy vegetation.

45. The Mulembwe Stream, between pools, 0.3 km below the road, 2.5 km NE of the Chingombe Catholic mission; 14°24.62' S, 29°59.25' E, 520 m a.s.l. — the bottom of the

Fig. 19. The temporary Mulembwe Stream with grassy and stony sections (photographs representative for loc. 39, 43, 45, 47), well defined in the stream bed at the end of the wet season (late-IV-2015) and broader, flooded during the peak of it (January 2017). *Pseudagrion kersteni, P. sublacteum, Paragomphus genei, Crocothemis divisa, C. sanguinolenta, Diplacodes luminans, Orthetrum brachiale, O. chrysostigma, Pantala flavescens Tramea basilaris, Trithemis arteriosa, T. kirbyi, Zygonyx torridus*.

Fig. 20. Stream pools on the temporary Mulembwe Stream at the end of the wet season (loc. 48, 22-IV-2015). *Agriocnemis exilis, Ischnura senegalensis, Pseudagrion hamoni, P. kersteni, P. sublacteum, Anax tristis, Crocothemis divisa, C. erythraea, C. sanguinolenta, Diplacodes luminans, Palpopleura deceptor, T. arteriosa, T. kirbyi* **(during the peak of the wet season, in January, also** *Nesciothemis farinosa, Pantala flavescens* **and** *Tramea basilaris***).**

rift valley. Temporary (existing in the rainy season), 0.2–1.5 m wide, several to 15 cm deep, flowing between grass and stones, locally more flooded and open (to 4 m wide) and stony, even with riffles. Sunny, surrounded by grassy areas and miombo woodlands.

46. A pool on the Mulembwe temporary stream, 0.4 km below the road, 2.5 km NE of the Chingombe Catholic mission; 14°24.65' S, 29°59.30' E, 520 m a.s.l. – the bottom of the rift valley. Temporary, small (75 m^2), shallow, with grassy vegetation.

47. The Mulembwe Stream, at the track, 2.65 km ENE of the Chingombe Catholic mission; 14°24.79' S, 29°59.43' E, 515 m a.s.l. — the bottom of the rift valley. Temporary (existing in the rainy season), 0.5–2 m wide, several to 15 cm deep, flowing between grass and stones, locally shallowly flooded and open (to 5 m wide) and stony, even with riffles. Sunny, surrounded by grassy areas and miombo woodlands (Fig. 19b).

48. A chain of stream pools on the Mulembwe Stream, at the airstrip, 3.1 km E of the Chingombe Catholic mission; 14°25.02' S, 29°59.72' E, 505 m a.s.l. — the bottom of the rift valley. Temporary, but quite persistent, existing mostly in the rainy season. Large, each 6–9 m wide and to 60 m long, 10–50 cm deep and warm. Almost stagnant, with hard or locally muddy bottom, in many places stony, in the shallow mouth sections more flowing and with many emergent large stones. Grassy vegetation overgrowing the whole breadth or only along shores and a few *Nymphaea caerulea*. Sunny, surrounded by grassy areas and miombo woodlands (Fig. 20).

49. A temporary pool in light miombo woodland, 2.7 km NE of the Chingombe Catholic mission; 14°24.37' S, 29°59.25' E, 520 m a.s.l. – the bottom of the rift valley. Small, shallow (to 50 cm), with an open water table bounded with herbaceous (mostly grassy) vegetation (Fig. 21 shows the pool in statu nascendi).

Fig. 21. A temporary pool in miombo woodland in statu nascendi in the early wet season (loc. 49, 19-XII-2013). *Anax tristis, Diplacodes luminans, Orthetrum brachiale, Palpopleura deceptor, Pantala flavescens* **(at the full-size pool during the peak and at the end of the wet season, in January and April, *Lestes ictericus* and *Pseudagrion hamoni*).**

50. Road puddles near the Bwingi Stream, 4.7 km NE of the Chingombe Catholic mission; 14°23.32' S, 29°59.78' E, 510–520 m a.s.l. – the bottom of the rift valley. Three large and quite deep puddles, temporary but existing for months in the rainy season; mostly bare, devoid of vegetation, but also including flooded roadsides with low vegetation. Sunny.

51. The lower complex of the Bwingi Stream, 5.2 km NE of the Chingombe Catholic mission; 14°23.14' S, 29°59.99' E, 510 m a.s.l. – the bottom of the rift valley. Complex of a permanent stream and its tributaries, seepages and temporarily flooded areas in its valley. The main stream is mostly shaded with clearings and morphologically strongly diversified between 0.5–1 m wide shallow sections with moderate current and almost stagnant stream pools to 2 m wide and 1 m deep (Fig. 22). In the stream bed, there is a mosaic of sandy-gravelly bottom and tree roots, abundant detritus and old leaves. The stream headwaters are more open and more strongly flowing with streamlets and seepages. In the stream valley, there are grassy depressions, partly shaded by loose trees and open fenny areas with seepages feeding the upper reaches of the stream. Their structure suggests that they may be temporarily flooded.

52. The upper complex of the Bwingi Stream, 5.1 km NE of the Chingombe Catholic mission; 14°23.00' S, 29°59.72' E, 520 m a.s.l. – the bottom of the rift valley. Complex of seepages and streamlets forming below the upper reaches of the main stream. Also, very small and probably temporary pools (to 20 cm deep) in moist to wet grassy areas with orange flowering orchids *Platycoryne mediocris*.

53. A nameless stream crossing a road, 7.5 km NE of the Chingombe Catholic mission; 14°21.99' S, 30°00.60' E, 530 m a.s.l. – the bottom of the rift valley. Permanent, 0.3–1 m wide, with warm water (fed by hot springs several hundred metres above), with a sandy bottom and detritus. Locally open and sunny, but mostly totally overgrown and 'roofed' with herbaceous vegetation.

54. The Fiperere Stream, lower reaches, 11.4 km NE of the Chingombe Catholic mission; 14°20.18' S, 30°01.72' E, 510 m a.s.l. – the bottom of the rift valley. Permanent, narrow (3–4 m), diversified: from deeper (to 40 cm) and calm sections with a sandy bottom to shallow and strong-current places with a stony bottom and rapids. 'Walls' of *Phragmites mauritianus* and patches of lower *Cyperus involucratus* along shores. Generally open and sunny, but locally (especially along shores) shaded by trees and high *Phragmites*. The stream bed is locally modified by gold mining.

55. The Kampoko River, a river ford on the road Chingombe–Mboroma, 26 km NE of the Chingombe Catholic mission; 14°14.33' S, 30°07.23' E (to 300 m downstream), 490 m a.s.l. – the bottom of the rift valley. At the very beginning of the rainy season, it is a small river ranging from 1 m wide watercourse with side puddles up to broader (10–20 m wide) calm river pools (Fig. 23); mostly shallow, with a sandy, gravelly or stony bottom with boulders and some detritus deposits. Partly shaded with trees and bushes overhanging the water, but mostly open.

56. The Mwenda River in Mwenda, 4.75 km SSW of the Chingombe Catholic mission; 14°27.59' S, 29°57.13' E, 495 m a.s.l. – the bottom of the rift valley. Permanent, highly diversified: from a few-metre-wide, shallow and strong-current section with riffles to open, wide (to 12–17 m), deeper and calm river pools; bottom deposits from stony within

Fig. 22. The Bwingi Stream flanked by gallery forest and fed by seepages (loc. 51), with (A) faster sections and (B) calm deep pools, at the beginning and at the end of the wet season (December 2013 and late-IV-2015). *Phaon iridipennis, Chlorocypha consueta, Platycypha caligata, Elattoneura glauca, Pseudagrion hageni, P. kersteni, Anax speratus, Crenigomphus hartmanni, Gomphidia quarrei, Paragomphus sabicus, Crocothemis sanguinolenta, Nesciothemis farinosa, Orthetrum abbotti, O. brachiale, O. hintzi, O. julia, Trithemis aconita, T. arteriosa, T. kirbyi, T. pluvialis.*

Fig. 23. The Kampoko River (loc. 55), strongly heterogenous morphologically, with (A) broad and (B) narrow sections at the beginning of the wet season (17-XII-2013). High species richness: *Phaon iridipennis, Platycypha caligata, Mesocnemis singularis, Pseudagrion acaciae, P. commoniae, P. kersteni, P. salisburyense, P. sublacteum, Anax speratus, Gomphidia quarrei, Ictinogomphus ferox, Brachythemis lacustris, Crocothemis erythraea, C. sanguinolenta, Diplacodes luminans, Nesciothemis farinosa, Olpogastra lugubris, Orthetrum chrysostigma, Pantala flavescens, Trithemis aconita, T. annulata, T. arteriosa, T. donaldsoni, Zygonoides fuelleborni, Zygonyx torridus*.

Fig. 24. The Mwenda River in Mwenda in the early wet season (loc. 56, 11-XII-2013). *Elatto-neura glauca, Pseudagrion sublacteum, Gomphidia quarrei, Brachythemis lacustris, Olpo-gastra lugubris, Orthetrum chrysostigma, Trithemis arteriosa, T. kirbyi, T. pluvialis, Zygon-oides fuelleborni, Zygonyx torridus*. Children efficiently 'hunting' for perching dragonflies (*O. chrysostigma* and *T. arteriosa)* with the use of *Phragmites mauritianus*-sticks. Many rapidly struck dragonflies were knocked down into the water.

rapids to muddy in stagnant pools. *Phragmites mauritianus* regularly along shores and locally entering the water. Open, sunny (Fig. 24).

57. The Tumbwe Stream in Tumbwe, 20.9 km SW of the Chingombe Catholic mission; 14°34.56' S, 29°51.54' E, 575 m a.s.l. – the bottom of the rift valley. Permanent, 2–5 metres wide, to 0.4 m deep, with a sandy, gravelly or stony bottom, and many thin roots of shore plants. Open, sunny.

58. The Lukusashi River, 7.9 km SE of the Chingombe Catholic mission; 14°27.52' S, 30°01.67' E (both riverbanks), 435 m a.s.l. – the bottom of the rift valley. Situated in hot open and semi-open landscapes, with bush and woodlands locally on the riverbanks. Fairly large to large: 40–200 m wide in the dry and wet season, respectively. Fairly fast-flowing with a variable water level: shallow and anastomosing within the broad riverbed at the end of the dry season and swollen in the rainy season. Bottom deposits mostly sandy, near banks more gravelly, and in side branches (calm or stagnant) sandy-muddy. In the low-water phase, almost without water vegetation, only with rare small patches of *Pistia stratiotes* and high 'walls' of *Phragmites mauritianus* at the border of water and riverbanks. In the high-water period, with broadly flooded bank vegetation.

59. The Lukusashi River, 8.1 km E of the Chingombe Catholic mission; 14°25.50' S, 30°02.51' E, 440 m a.s.l. – the bottom of the rift valley (Fig. 25). For the habitat descrip-tion, see [58.].

60. Two temporary pools (60 m distant) in a large meandering ravine, which is a product of temporary watercourse erosion, 150–200 m from the Lukusashi River, 8.1 km E

Fig. 25. The Lukusashi River (loc. 59) in the low-water phase in the beginning of the wet season (15 and 19-XII-2013). (A) a general view of the anastomosing river with its side having more stagnant bays and branches, (B) a view from the sandy main current on an eroded 10–14-metre-high riverbank with mopane woodland. *Mesocnemis singularis, Pseudagrion acaciae, P. glaucescens, P. hamoni, P. sublacteum, Gomphidia quarrei, Ictinogomphus ferox, Mastigogomphus cf. dissimilis, Paragomphus elpidius, Brachythemis lacustris, B. leuco-sticta, Diplacodes lefebvrii, D. luminans, Nesciothemis farinosa, Olpogastra lugubris, Trithemis annulata, T. arteriosa, T. kirbyi, Urothemis assignata, Zygonoides fuelleborn*i.

Fig. 26. A temporary turbid pool in a ravine in the proximity of the Lukusashi River in the mid-rainy season (loc. 60, 21-I-2017). Tetrathemis polleni, *Orthetrum brachiale.*

of the Chingombe Catholic mission; 14°25.38' S, 30°02.50' E, 450 m a.s.l. – the bottom of the rift valley. Situated in semi-open landscape, at the base of the ravine wall. Small, mostly sunny, but partly shaded by dense bushes with branches overhanging the water table. With a soft clayey bottom and turbid shallow water (Fig. 26).

61. Miombo woodlands and a clearing by a ravine, 0.2–0.4 km of the Lukusashi River, 8.1 km E of the Chingombe Catholic mission; 14°25.30' S, 30°02.49' E, 450 m a.s.l. – the bottom of the rift valley.

62. The Lukusashi River and the mouth of the Bwingi Stream, 8.5 km of the Chingombe Catholic mission; 14°25.41' S, 30°02.70' E, 440 m a.s.l. – the bottom of the rift valley. For the riverine habitat description, see [58.]. Additionally, the sandy-to-stony mouth section of the stream varying between swollen in the rainy season and completely dried up in the dry season.

63. The Lunsemfwa River at the ferry on the Kabwe–Old Mkushi road; 14°18.45' S, 29°07.46' E, 1,060 m a.s.l. – the plateau outside the main area of study; fairly large (20–90 m wide), deep and calm, locally anastomosing, with wooded shores and islands.

64. Kabwe, Missionary Sisters of the Holy Family; 14°26.72' S, 28°27.60' E, 1,205 m a.s.l. – the plateau outside the main area of study; gardens in a large town; dragonflies allochthonous, possibly originating from ponds or water bodies in old exploitation pits in other parts of the town.

65. Kabwe-Natuseko, a clay pit; 14°24.02' S, 28°27.65' E, 1,180 m a.s.l. – the plateau outside the main area of study; a large and deep pond in the post-exploitation pit.

Along the shores, dense Typha sp. and high *Phragmites mauritianus* with admixture of *Persicaria senegalensis*; locally on the water table, floating carpets of *Ludwigia adscendens* subsp. *diffusa* and scattered *Nymphaea caerulea*. Also, several small temporary clay pools and puddles, mostly bare, without vegetation. Open, sunny.

66. A tributary of the Mulungushi River near the Great North Road Kabwe–Kapiri Mposhi, 17.5 km NW of Kabwe; 14°19.10' S, 28°32.81' E, 1,125 m a.s.l. – the plateau outside the main area of study. An open small very sluggish river with flooded valley (a few to 20 m wide). With thick, soft bottom deposits and water up to 1 m deep, almost completely overgrown with dense herbaceous vegetation.

Methods

A set of habitats studied in the main study area included water bodies situated within a short operational range from the base in Chingombe. To make this habitat set representative and to identify the odonate assemblages in the particular habitats we visited all water bodies on the bottom of the rift valley and some localities accessible in the mountains and on the upland plateau. Along the selected watercourses, we studied several localities to find an intra-habitat odonate diversity corresponding to diverse habitat conditions, and to describe an odonatological river-continuum.

Many localities were intentionally visited several times not only to complete their species lists but also to recognise phenology of the odonate assemblages of the studied habitats. We paid particular attention to a comparison between three phases of the wet season: its beginning, height and end.

In each locality, we used standard research procedures. We searched for odonates both at the water and in its proximity (we also studied several localities far from the water). We focused on the observation of imagines, also with the use of binoculars, and we paid attention to all aspects suggesting the species' native occurrence, such as teneral and juvenile individuals, the reproductive behaviour and territorial/patrolling ♂♂. We also tried to assess the abundance of each species. The specimens collected with a hand net were preserved in ethyl alcohol (in tubes) or dehydrated in acetone and stored in envelopes in plastic containers. We described habitats in detail, searching particularly for relations between species and habitat elements/traits. Documentation consisted of notes recorded in the voice recorder and very numerous photographs of both the habitats and species.

The collected individuals are in the collection of Rafał Bernard in the Nature Collections at the Faculty of Biology, Adam Mickiewicz University in Poznań, Poland.

Results

Species

In total, 107 species were recorded: 104 in the main area of study (Chingombe) and 21 at episodically visited localities in other areas (Kabwe and Lunsemfwa), with three species (*Hemistigma albipunctum, Rhyothemis semihyalina* and *Trithemis nuptialis*) found only

there. We collected and presented 804 records (species/locality/day): 777 in the main area of study (Chingombe) and 27 in other areas (25 Kabwe and its environs, 2 Lunsemfwa). The list of records given below includes all the collected data, but all analyses and comments in the next subchapters only concern the main study area (loc. [1–62]).

For 23 species previously analysed taxonomically or/and zoogeographically, asterisks were added after the species names. They refer to the corresponding publications: * Bernard & Daraż 2018, ** Bernard et al. 2018.

Males are abbreviated to ♂, females to ♀ and exuviae to Ex. All collected individuals are given in brackets. An entry "30-IV-2015, (4♂♂)" means that four males were observed and collected. Another kind of entry, "25-IV-2015, 3♂♂ (2♂♂)" means that three males were observed and two of them were collected. Entries "(ExM)" and "(ExF)" mean a collected male and female exuviae, respectively.

Rich photodocumentation was also collected, but it is only mentioned exceptionally (as "phot.") i.e. when an uncommon species was not collected and (convincingly) recognised in the field, but conclusively identified post-factum on a photograph.

Lestes amicus Martin, 1910
[1.] 20-XII-2013, (2♂♂); 31-I-2017, (1♂). [3.] 30-IV-2015, (1 teneral ♂).

Lestes dissimulans Fraser, 1955
[1.] 20-XII-2013, after first intensive rains but still without water, already reproductive activity (6♂♂, 1♀, including 1 tandem); 31-I-2017, (2♂♂). [3.] 30-IV-2015, (1 teneral ♂).

Lestes ictericus Gerstäcker, 1869 *
[38.] 29-I-2017, emergence: 9 teneral individuals (3♂♂). [49.] 21-IV-2015, emergence: several teneral individuals (2♂♂, 1♀); 29-I-2017, emergence: several teneral individuals (1♂).

Lestes plagiatus (Burmeister, 1839)
[2.] 5-XII-2013, (1♂). [3.] 30-IV-2015, (4♂♂, including 2 teneral and 1 immature). [35.] 18-XII-2013, (2♂♂) at the pond and streamlet pool; 17-IV-2015, (1♂).

Lestes virgatus (Burmeister, 1839)
[1.] 20-XII-2013, (1♂); 31-I-2017, (2♂♂, 1♀, including 1 tandem). [3.] 30-IV-2015, (1 teneral ♂).

Phaon iridipennis (Burmeister, 1839)
[5.] 5-XII-2013, 1 individual. [15.] 7-XII-2013, 1 individual. [16.] 7-XII-2013, 3–4 individuals (1♂); 19-IV-2015, 2 ♀♀ (1♀). [19.] 7-XII-2013, 2 individuals. [23.] 23-I-2017, (1♂). [25.] 23-I-2017, 1 individual. [27.] 14-XII-2013, 2♂♂. [28.] 6-XII-2013, 3 individuals (1♂); 13-XII-2013, several individuals, including at least 2♂♂, in open places (overcast!). [29.] 15-IV-2015, (1♂). [30.] 14-IV-2015, (1♂, 1♀); 24-IV-2015, 1 teneral individual. [33.] 14-XII-2013, 1 individual. [35.] 16-XII-2013, 1 individual (vagrant?). [51.] 23-IV-2015, (1♂, 1♀). [53.] 12-XII-2013, 1 individual. [54.] 17-XII-2013, 1 individual. [55.] 17-XII-2013, numerous after rainfall in overcast weather (1♂).

Chlorocypha consueta (Karsch, 1899) (Fig. 27)
[4.] 5-XII-2013, (2♂♂, 1♀). [5.] 30-IV-2015, 1♂. [7.] 26-I-2017, 1♂; 28-I-2017, 1♂. [8.] 28-

IV-2015, numerous individuals (1♂). [9.] 25-IV-2015, very numerous individuals in an optimal habitat (2♂♂); 28-IV-2015, numerous individuals (1♀). [11.] 26-I-2017, 1♂. [12.] 25-IV-2015, 3♂♂ (2♂♂); 26-I-2017, (3♂♂, including 1 teneral, 1 immature). [14.] 20-I-2017, 2♂♂. [16.] 7-XII-2013, (2♂♂); 19-IV-2015, 3♂♂. [19.] 16-XII-2013, 3♂♂ (1♂); 19-I-2017, 1♂. [21.] 11-IV-2015, 2♂♂ (1♂). [23.] 23-I-2017, 2♂♂ (1♂). [25.] 23-I-2017, 5 ♂♂ (1♂). [51.] 23-IV-2015, 2♂♂.

Fig. 27. *Chlorocypha consueta*, male (25-IV-2015).

Platycypha caligata (Selys, 1853)
[16.] 19-IV-2015, 3♂♂; 20-I-2017, tandem in copula. [18.] 16-XII-2013, 2♂♂ (1♂); 19-I-2017, 1♂. [19.] 7-XII-2013, 3♂♂ (1♂); 16-XII-2013, several individuals (1♂, 2♀♀). [21.] 11-IV-2015, numerous individuals. [23.] 23-I-2017, (1♂). [25.] 23-I-2017, 1♂. [27.] 14-XII-2013, 1♂, 1♀. [28.] 6-XII-2013, numerous individuals, ♂♂ and ♀♀, both mature and immature (2♂♂: 1 adult, 1 immature, 1♀); 13-XII-2013, numerous individuals, ♂♂ and ♀♀; 24-IV-2015, 7♂♂, 2♀♀ (1♂). [30.] 15-I-2017, 2♂♂, 1 tandem. [33.] 14-XII-2013, 1♂; 13-IV-2015, 2♂♂, 1♀ (1♂). [51.] 9-XII-2013, 3♂♂ at the Bwingi stream (1♂); 23-IV-2015, (1 immature ♂). [54.] 17-XII-2013, 1♂, 1♀ (1♂). [55.] 17-XII-2013, 2♂♂ (1♂).

Allocnemis marshalli (Ris, 1921) *
[7.] 26–28-I-2017, several individuals, mostly teneral/juvenile, but also adult (2 ♂♂: teneral and adult). [8.] 28-IV-2015, 2 adults (1♂). [9.] 25-IV-2015, (1♂, 1♀); 28-IV-2015, (1♀). [11.] 26-I-2017, 4 tandems, including 2 ovipositing, and 1♀ (1♂ and 1♀), mostly in the widest (1.5 m) and shallowest, partly sunny section, attracted by favourable oviposition conditions. [13.] 20-I-2017, 2 ♂♂, 1♀ (1♂, 1♀). [17.] 19-I-2017, (1♀).

Elattoneura cellularis (Grünberg, 1902) (Fig. 28)
[7.] 27-I-2017, 1♂, 1 tandem (2 ♂♂); 28-I-2017, 1♂, 1 tandem (1♂, 1♀). [8.] 28-IV-2015, (2 ♂♂). [9.] 25-IV-2015, (2 ♂♂); 28-IV-2015, (2 ♂♂, 1♀, including 1 tandem). [16.] 7-XII-2013, (1♂). [23.] 23-I-2017, (1♂) and several probable individuals. [25.] 23-I-2017, (1♂) and 1–2 probable individuals.

Fig. 28. *Elattoneura cellularis*, **male (28-IV-2015).**

Fig. 29. *Elattoneura glauca*, **male (13-IV-2015).**

Elattoneura glauca (Selys, 1860) (Fig. 29)

[11.] 26-I-2017, (1♂). [14.] 20-I-2017, (1 teneral ♂). [16.] 19-IV-2015, (1♂) in semi-open place with Cyperus involucratus. [17.] 19-I-2017, (1♂). [18.] 7-XII-2013, (2 ♂♂, 1♀, including 1 tandem). [19.] 16-XII-2013, 1♂, 1 tandem. [28.] 6-XII-2013, 2 ♂♂ (1♂); 13-XII-2013, 1♂; 24-IV-2015, (1♂, 1♀ in tandem). [29.] 15-IV-2015, (1♂). [33.] 13-XII-2013, 1♂; 14-XII-2013, 2 ♂♂; 13-IV-2015, (1♂). [35.] 14-XII-2013, (1♂); 16-XII-2013, 1♂; 18-XII-2013, 1♂ at the temporary streamlet. [37.] 30-I-2017, (1♂). [51.] 9-XII-2013, fairly numerous individuals at the stream, 1 tandem (1♂); 12-XII-2013, c. 10 individuals, both at the main stream and in the streamlet-seepage areas (2 ♂♂); 16-IV-2015, several individuals, including 1 tandem, also in the seepage zone (1♂); 23-IV-2015, numerous individuals (1♂). [53.] 12-XII-2013, 5 ♂♂ (2 ♂♂). [54.] 17-XII-2013, (1♂). [56.] 10-XII-2013, (1♂). [57.] 10-XII-2013, 2 ♂♂ (1♂).

Mesocnemis singularis Karsch, 1891

[55.] 17-XII-2013, 1♂. [56.] 10-XII-2013, 1♂. [59.] 15-XII-2013, 3♂♂ (1♂); 19-XII-2013, 2♂♂ (1♂).

Aciagrion africanum Martin, 1908 *

[1.] 20-XII-2013, after first intensive rains but still without water, (3♂♂, 1♀). [3.] 30-IV-2015, (3♂♂, 1♀, including 1 tandem and 1 teneral ♂): both emergence and reproductive activity.

Africallagma fractum (Ris, 1921)

[1.] 20-XII-2013, after first intensive rains but still without water, several individuals, 1 tandem (4♂♂, one from the tandem). [3.] 30-IV-2015, (2♂♂). [35.] 17-IV-2015, 3♂♂ at the pond (2♂♂). [37.] 23-I-2017, (1♂).

Fig. 30. *Africallagma pallidulum*, male (9-XII-2013).

Fig. 31. *Agriocnemis exilis***, male (21-IV-2015).**

Fig. 32. *Ceriagrion kordofanicum***, male (8-XII-2013).**

Fig. 33. *Ceriagrion whellani***, male (18-XII-2013).**

Africallagma pallidulum Dijkstra, 2007 * (Fig. 30)

[1.] 20-XII-2013, after first intensive rains but still without water, (2♂♂). [35.] 16-XII-2013, (1♀). [51.] In moderate numbers, except for one ♀ in a very restricted area of the stream valley still without water, recorded on 9-XII-2013, (2♂♂), 12-XII-2013, (1♀), 17-XII-2013, (3♂♂), and 19-XII-2013, (3♂♂, 2♀♀).

Agriocnemis exilis Selys, 1872 (Fig. 31)

[3.] 30-IV-2015, (2 ♂♂, including 1 teneral). [37.] 23-I-2017, (1♂); 30-I-2017, an adult ♂ and emergence of 5 individuals (1♂). [38.] 16-IV-2015, emergence, 7 teneral individuals (2 ♂♂, 2♀♀); 21-IV-2015, 1♂, 1♀; 27-IV-2015, 2 teneral individuals; 29-IV-2015, teneral individuals. [44.] 20-IV-2015, (1 teneral ♂). [48.] 22-IV-2015, ca 10 individuals at three stream pools (2 ♂♂). [56.] 10-XII-2013, (1♂) at a broader river pool.

Agriocnemis gratiosa Gerstäcker, 1891

[35.] 10-IV-2015, 4 ♂♂ at the pond (3♂♂).

Ceriagrion banditum Kipping & Dijkstra, 2015 *

[1.] 20-XII-2013, after first intensive rains but still without water, 1♂, 1 tandem (2 ♂♂, 1♀); 31-I-2017, several individuals, 1 tandem (5 ♂♂, 2♀♀). [3.] 30-IV-2015, (1 teneral ♂). [35.] 16-XII-2013, 1♂ at the pond (phot., data not included in Bernard & Daraż 2018); 18-XII-2013, (1♂). [44.] 20-IV-2015, (1 teneral ♂).

Ceriagrion glabrum (Burmeister, 1839)

[1.] 31-I-2017, (1♂). [3.] 30-IV-2015, (4 ♂♂, including 2 teneral). [33.] 13-XII-2013, (1♂). [35.] 14-XII-2013, 2 ♂♂ at the pond (1♂); 16-XII-2013, (1♂, 1♀ in tandem) at the pond. [38.] 27-IV-2015, 1 teneral ♂.[65.] 13-I-2017, (2 ♂♂). [66.] 13-I-2017, several individuals (4 ♂♂).

Ceriagrion kordofanicum Ris, 1924 * (Fig. 32)

[58.] 8-XII-2013, 3♂♂ (2♂♂).

Ceriagrion mourae Pinhey, 1969 **

[38.] 20-IV-2015, (1 teneral ♂); 21-IV-2015, (1 teneral ♂); 23-IV-2015, (2 ♂♂, 1♀, the ♀ confirmed genetically), additionally two probable individuals observed: 1 teneral ♂ and 1 teneral ♀; 16-I-2017, (3 ♂♂); 17-I-2017, (1♂, 1♀ in tandem).

Ceriagrion suave Ris, 1921

[38.] 21-IV-2015, (2 ♂♂, 1♀, including 1♂ and 1♀ teneral); 23-IV-2015, 1 teneral ♂ (phot.); 27-IV-2015 1 teneral ♂ (phot.).

Ceriagrion whellani Longfield, 1952 (Fig. 33)

[10.] 28-IV-2015, 5 ♂♂, 1 tandem (3♂♂, 1♀, including the tandem); 26-I-2017, 1♂. [35.] 18-XII-2013, (2♂♂, 2♀♀, including 1 tandem) at the sluggish temporary stream. [37.] 30-I-2017, 1♂. [51.] 16-IV-2015, (1♂) in a seepage-streamlet zone.

Ischnura senegalensis (Rambur, 1842)

[48.] 22-IV-2015, (1♂). [65.] 13-I-2017, more than 5 ♂♂ (1♂).

Pseudagrion acaciae Förster, 1906

[28.] 6-XII-2013, several individuals (1♂). [50.] 25-I-2017, 2♂♂ (1♂), allochthonous? [55.] 17-XII-2013, (1♂). [58.] 8-XII-2013, fairly numerous ♂♂, 1 tandem (3♂♂, 1♀); 12-IV-2015,

Fig. 34. *Pseudagrion commoniae*, **tandem, oviposition (15-IV-2015).**

Fig. 35. *Pseudagrion gamblesi*, **male (13-XII-2013).**

Fig. 36. *Pseudagrion glaucescens*, **male (19-XII-2013).**

(1♂). [59.] 15-XII-2013, (2♂♂, 1♀, including 1 tandem); 19-XII-2013, 1♂; 21-I-2017, 3♂♂ (1♂). [61.] 24-I-2017, numerous individuals in the mouth zone of the temporary stream and in the adjacent woodland. [62.] 21-I-2017, 1♂ at the temporary stream near the Lukusashi River; 24-I-2017, 1♂ in the temporary stream mouth.

Pseudagrion commoniae (Förster, 1902) * (Fig. 34)

[29.] 15-IV-2015, fairly numerous, tandems (4 ♂♂, 1♀), an immature ♂ caught and consumed by ♂ of Pseudagrion gamblesi. [34.] 14-IV-2015, (1♂). [35.] 14-XII-2013, 3 ♂♂ above the water table of the pond (2 ♂♂); 16-XII-2013, 1♂ at the pond (data not included in Bernard & Daraż 2018). [38.] 29-I-2017, (1♂ donated to the collection of Jens Kipping). [46.] 21-IV-2015, (1 teneral ♂). [51.] 12-XII-2013, (1 teneral ♂) probably originating from the stream. [55.] 17-XII-2013, several ♂♂ above the water table of wide and calm sections of the river (3 ♂♂).

Pseudagrion gamblesi Pinhey, 1978 (Fig. 35)

[23.] 23-I-2017, 1♂. [26.] 23-I-2017, 1♂. [27.] 14-XII-2013, (1♂). [28.] 6-XII-2013, 1♂, 3♀♀ (1♂, 2♀♀); 13-XII-2013, 4 ♂♂, 2♀♀ (3 ♂♂, 1♀, including juvenile 1♂ and 1♀), more active and more easily detectable than usually due to the subdued sunshine and overcast weather. [29.] 15-IV-2015, 2 ♂♂, 1♀ (1♂, 1♀), one of the ♂♂ consuming an immature ♂ of *P. commoniae*. [33.] 13-XII-2013, (1♂); 14-XII-2013, (1♀); 13-IV-2015, (1♂, 1♀). [54.] 17-XII-2013, 1♂.

Pseudagrion glaucescens Selys, 1876 (Fig. 36)

[59.] 15-XII-2013, 4 ♂♂ (3♂♂); 19-XII-2013, (1♂).

Pseudagrion hageni Karsch 1893 (ssp. tropicanum) (Fig. 37)

[7.] 28-I-2017, 2♂♂ (1♂). [8.] 28-IV-2015, 2♂♂. [9.] 25-IV-2015, 2♂♂ (1♂). [11.] 26-I-2017, 1♂. [14.] 20-I-2017, 3♂♂ (1♂). [16.] 19-IV-2015, 3♂♂, 1 tandem (3♂♂, 1♀). [20.] 11-IV-2015, 1♂. [23.] 23-I-2017, (1♂). [33.] 13-IV-2015, (1♂). [35.] 16-XII-2013, fairly numerous ♂♂ and 2 tandems at the temporary stream (3♂♂, 1♀, including 1 tandem); 18-XII-2013, several individuals and 1 submerging tandem with an ovipositing ♀ at the temporary stream (1♂, 1♀); 17-IV-2015, (2 teneral ♂♂) at the temporary stream. [51.] 23-IV-2015, several ♂♂ (2♂♂).

Pseudagrion hamoni Fraser, 1955

[1.] 31-I-2017, (1♂). [3.] 30-IV-2015, (2♂♂, including 1 teneral). [29.] 15-IV-2015, 2♂♂ (1♂). [37.] 30-I-2017, 2♂♂ (1♂). [38.] 20-IV-2015, (1 teneral ♂); 21-IV-2015, (2 teneral ♂♂); 27-IV-2015, (1 teneral ♂). [44.] 20-IV-2015, (1 teneral ♂). [46.] 21-IV-2015, (1 teneral ♂). [48.] 22-IV-2015, (1 teneral ♂); 17-I-2017, (1♂). [49.] 29-I-2017, 2♂♂ (1♂). [50.] 25-I-2017, (1♂). [56.] 10-XII-2013, (1♂). [59.] 15-XII-2013, several ♂♂ and 1 tandem (3♂♂, 1♀); 19-XII-2013, (1♂). [65.] 13-I-2017, (1♂).

Pseudagrion kersteni (Gerstäcker, 1869)

[3.] 30-IV-2015, (6♂♂, including 1 teneral and 3 immature) in the area with a streamlet and trickles. [9.] 25-IV-2015, 1–2♂♂. [16.] 19-IV-2015, 2♂♂. [18.] 7-XII-2013, uncommon; 20-I-2017, 2♂♂. [19.] 7-XII-2013, several ♂♂ and 1 tandem (4♂♂); 19-I-2017, in moderate numbers. [21.] 11-IV-2015, numerous individuals. [27.] 14-XII-2013, 4♂♂. [28.] 6-XII-2013, several ♂♂ (1♂); 13-XII-2013, uncommon; 10-IV-2015, (1♂); 24-IV-2015, numerous

Fig. 37. *Pseudagrion hageni*, submerged oviposition in four acts (18-XII-2013).

Fig. 38. *Pseudagrion sjoestedti*, male (13-XII-2013).

individuals (2♂♂). [29.] 15-IV-2015, (1♂). [30.] 14-IV-2015, (1♂). [33.] 14-XII-2013, 2♂♂; 13-IV-2015, numerous individuals and tandem in copula (1♂, 1♀). [35.] 14-XII-2013, 2♂♂

(1♂), 1 of them at puddles in the streambed of a temporary watercourse being in statu nascendi; 16-XII-2013, 2♂♂ and 2 tandems, at both the temporary stream and pond; 18-XII-2013, 1♂. [37.] 23-I-2017, numerous individuals at the trickle feeding ponds; 30-I-2017, 1♂. [39.] 29-I-2017, 2♂♂ (1♂). [48.] 22-IV-2015, (1♂); 17-I-2017, 1 tandem. [51.] 9-XII-2013, 2–3♂♂; 12-XII-2013, several individuals, also in the seepage-streamlet zones (5♂♂); 16-IV-2015, 4♂♂, mostly in the seepage-streamlet zone (2♂♂); 23-IV-2015, several ♂♂ (2♂♂, 1 of them teneral). [52.] 25-I-2017, 2♂♂ in the seepage-streamlet zone. [53.] 12-XII-2013, (2♂♂, 1♀). [54.] 17-XII-2013, (1♂). [55.] 17-XII-2013, 1♂. [57.] 10-XII-2013, fairly numerous individuals (1♂). [66.] 13-I-2017, (1♂).

Pseudagrion salisburyense Ris, 1921
[55.] 17-XII-2013, (1♂).

Pseudagrion sjoestedti Förster, 1906 (Fig. 38)
[18.] 16-XII-2013, (1♂). [19.] 7-XII-2013, 1♂. [23.] 23-I-2017, (1♂). [27.] 14-XII-2013, (1♂). [28.] 13-XII-2013, (1♂). [30.] 15-I-2017, 1♂. [33.] 14-XII-2013, (1♂); 13-IV-2015, (2♂♂, 1♀, including 1 tandem). [37.] 23-I-2017, (1♂). [54.] 17-XII-2013, (1♂).

Pseudagrion spernatum Selys, 1881
[7.] 27-I-2017, (1♂).

Pseudagrion sublacteum (Karsch, 1893)
[28.] 6-XII-2013, 2♂♂ (1♂); 13-XII-2013, 2♂♂ (1♂); 24-IV-2015, 5♂♂ and 1 tandem (1♂). [29.] 15-IV-2015, 2♂♂ (1♂). [33.] 13-XII-2013, (1 teneral ♂); 13-IV-2015, co-dominant, numerous ♂♂, 1 tandem (2♂♂). [39.] 29-I-2017, 1♂, 1 tandem (1♂, 1♀). [48.] 22-IV-2015, (1 teneral ♂). [49.] 29-I-2017, 1♂ (vagrant?). [52.] 25-I-2017, (1♂, 1♀ in tandem) in the seepage-streamlet zone. [53.] 12-XII-2013, (5♂♂, 1♀, including 1 juvenile ♂ and 1 tandem). [55.] 17-XII-2013, 1 tandem (1♂). [56.] 10-XII-2013, fairly numerous ♂♂, 1 tandem (2♂♂, 1♀, including 1 tandem). [57.] 10-XII-2013, (1♂). [59.] 15-XII-2013, (1♂, 1♀ in tandem); 19-XII-2013, 1♂.

Anax ephippiger (Burmeister, 1839)
[1.] 20-XII-2013, 1 individual. [30.] 11-XII-2013, crepuscular activity: 5 individuals foraging, including at least 2♀♀ (1♂, 1♀). [38.] 27-IV-2015, 1 ExM.

Anax imperator Leach, 1815
[3.] 30-IV-2015, 1♂. [35.] 14-XII-2013, 1♂. [56.] 10-XII-2013, 1 territorial ♂ at the river pool.

Anax speratus Hagen, 1867
[2.] 5-XII-2013, 1 patrolling ♂. [4.] 5-XII-2013, 1♂. [7.] 28-I-2017, 2 larvae collected in stream pools and reared, emerged in Poland (1 teneral ♂, 1 teneral ♀, 2 Ex). [18.] 7-XII-2013, 2♂♂ (1♂); 16-XII-2013, (1♂). [28.] 24-IV-2015, 1♂. [29.] 15-IV-2015, 1 patrolling ♂. [48.] 22-IV-2015, 1 individual at the stream pool (vagrant?). [51.] 9-XII-2013, 1 patrolling ♂. [55.] 17-XII-2013, 1 individual.

Anax tristis Hagen, 1867
[1.] 20-XII-2013, 2♂♂ (1♂). [35.] 18-XII-2013, 1♂, 2♀♀ (the former ovipositing in the pond and the latter searching for an oviposition site in the temporary stream). [38.] 16-I-2017, 1♂ foraging in an open area; 17-I-2017, 1 individual several times at the pool. [41.] 16-

I-2017, 1 territorial ♂ above the large puddle (1♂). [48.] 22-IV-2015, 1 ExM. [49.] 19-XII-2013, 2♂♂, 1♀ (1♂).

Gynacantha immaculifrons Fraser, 1956 *
[30.] 11-XII-2013, (1♀); 10-IV-2015, (1♂, 1♀); 23-IV-2015, (1♂); all the individuals during the crepuscular activity, foraging in the same very small area of 400 m².

Gynacantha manderica Grünberg, 1902
[3.] 30-IV-2015, (1 teneral ♂) in the maiden flight near a streamlet flooding under a tree.

Gynacantha vesiculata Karsch, 1891 *
[30.] 27-IV-2015, (1 foraging ♂, crepuscular activity).

Gynacantha villosa Grünberg, 1902 *
[30.] 22-IV-2015, (1 foraging ♂); 26-IV-2015, (1 foraging ♀); both individuals during the crepuscular activity.

Gynacantha sp. (nov.) (the second species hidden within the present name *G. villosa*) *
[30.] 15-IV-2015, (1 foraging ♀, crepuscular activity).

Heliaeschna fuliginosa Selys, 1883 *
[7.] 26-I-2017, 2 ovipositing ♀♀ (1♀); 28-I-2017, 3–4 ovipositing ♀♀ (1♀).

Heliaeschna trinervulata Fraser, 1955 *
[30.] 16-IV-2015, (1♀); 18-IV-2015 (1♂); 23-IV-2015 (1♀); all individuals juvenile, foraging (crepuscular activity).

Crenigomphus hartmanni (Förster, 1898)
[19.] 7-XII-2013, (1 juvenile ♀); 16-XII-2013, (1♀) at some distance from the stream. [24.] 23-I-2017, 1 individual. [29.] 15-IV-2015, (1 teneral ♀ + its exuviae). [32.] 22-I-2017, (1♂, 1♀). [33.] 22-I-2017, (1♀). [51.] 9-XII-2013, (2♀♀, including 1 juv.).

Fig. 39. *Gomphidia quarrei*, male (6-XII-2013).

Gomphidia quarrei (Schouteden, 1934) (Fig. 39)

[19.] 7-XII-2013, 3♂♂ (1♂). [22.] 23-I-2017, 1♂. [23.] 23-I-2017, 1 individual. [27.] 14-XII-2013, 1♂. [28.] 6-XII-2013, at least 4♂♂ (1♂). [30.] 13-XII-2013, (1♂). [31.] 22-I-2017, (1♂). [32.] 22-I-2017, 2 ♂♂, 1♀. [33.] 14-XII-2013, 1 individual; 22-I-2017, 1 individual. [51.] 9-XII-2013, (1♀) at the stream. [55.] 17-XII-2013, 1 individual. [56.] 10-XII-2013, 1♂. [59.] 15-XII-2013, 1 individual.

Ictinogomphus ferox (Rambur, 1842)

[18.] 7-XII-2013, (1♂). [19.] 7-XII-2013, 1♂. [33.] 14-XII-2013, 1 individual. [55.] 17-XII-2013, 2 patrolling ♂♂, 1 tandem and several exuviae on a log, boulders and *Phragmites mauritianus*, all at the broader section of the watercourse – the river pool (1♂, 1♀, 2 ExM, 4 ExF). [56.] 10-XII-2013, several individuals with at least 2 ♂♂, mostly at the broader more stagnant sections of the river (1♂). [59.] 15-XII-2013, 1♂. [63.] 5-XII-2013, 1♂.

Lestinogomphus angustus Martin, 1912
[28.] 6-XII-2013, 1 individual; 13-XII-2013, 2♂♂ (1 teneral ♂). [31.] 22-I-2017, 1 tandem (1♂, 1♀).

Mastigogomphus cf. *dissimilis* (Cammaerts, 2004) *
[59.] 15-XII-2013, 1 ExF.

Notogomphus cf. *zernyi* (St. Quentin, 1942) *
[15.] 7-XII-2013, (1 teneral ♀).

Paragomphus cognatus (Rambur, 1842) (Fig. 40)
[7.] 26-I-2017, (1♂). [31.] 22-I-2017, (1♀). [33.] 22-I-2017, (1♂).

Fig. 40. *Paragomphus cognatus*, male (22-I-2017).

Paragomphus elpidius (Ris, 1921)
[31.] 22-I-2017, (1♂). [33.] 22-I-2017, (1♀). [59.] 19-XII-2013, (1 ovipositing ♀).

Paragomphus genei (Selys, 1841)
[19.] 16-XII-2013, (1♀) at some distance from the stream (autochthonous?). [31.] 9-XII-2013, (1♀). [42.] 16-I-2017, 4♂♂ at the stream (1♂). [45.] 17-I-2017, 1 individual. [47.] 17-I-2017, 1 individual. [50.] 25-I-2017, 2♂♂ and 1 probable ♀ at two puddles (2 ♂♂). [51.] 17-XII-2013, (1♂) in the seepage-streamlet zone. [61.] 24-I-2017, (1♀).

Paragomphus sabicus Pinhey, 1950
[51.] 9-XII-2013, several individuals, both ♂♂ and ♀♀, at two sites (1♂, 2♀♀, two of them juvenile); 12-XII-2013, (1♀). [61.] 24-I-2017, (1♀) in a bush far from the river, assigned to it as to the nearest water, but the origin of the individual unresolved.

Phyllomacromia monoceros (Förster, 1906) *
[7.] 26-I-2017, 3♂♂, one of them foraging (2♂♂); 27-I-2017, (1♀); 28-I-2017, (1♂).

Phyllomacromia picta (Hagen in Selys, 1871) (Fig. 41)
[31.] 24-IV-2015, 1 foraging ♂ (1♂); 22-I-2017, 2♂♂ (1♂).

Fig. 41. *Phyllomacromia picta*, male (22-I-2017).

Acisoma inflatum Selys, 1882
[1.] 31-I-2017, (1♂).

Aethiothemis bequaerti Ris, 1919
[3.] 30-IV-2015, (1 teneral ♂, 1♀).

Aethiothemis solitaria Ris in Martin, 1908
[3.] 30-IV-2015, (1♂).

Fig. 42. *Brachythemis lacustris***, a 'sociable' obelisk position (8-XII-2013).**

Brachythemis lacustris (Kirby, 1889) (Fig. 42)
[55.] 17-XII-2013, 2 ♂♂, 1♀. [56.] 10-XII-2013, (1♂, 1♀). [57.] 10-XII-2013, (1♀). [58.] 8-XII-2013, numerous: at least several dozen individuals (2 ♂♂, 1♀); 12-IV-2015, 7–8 ♂♂, 2–3♀♀. [59.] 15-XII-2013, numerous individuals, both ♂♂ and ♀♀ (1♂, 1♀); 21-I-2017, several individuals, both ♂♂ and ♀♀. [60.] 21-I-2017, 2♂♂ from the river.

Brachythemis leucosticta (Burmeister, 1839)
[58.] 8-XII-2013, 1♂; 12-IV-2015, (1♂). [59.] 15-XII-2013, (2♂♂, including 1 immature). [62.] 21-I-2017, several individuals. [65.] 13-I-2017, several individuals, both ♂♂ and ♀♀ (1♂).

Bradinopyga cornuta Ris, 1911 (Fig. 43)
[31.] 18-I-2017, (1♂). [32.] 22-I-2017, 5 ♂♂ (1♂).

Crocothemis divisa Baumann, 1898 (Fig. 44)
[36.] 10-IV-2015, (1 teneral ♀); 18-IV-2015, (1♂). [39.] 16-IV-2015, (1♂). [43.] 16-IV-2015, (1♂). [45.] 21-IV-2015, 1♂. [48.] 22-IV-2015, 2♂♂, 1♀ (1♂).

Crocothemis erythraea (Brullé, 1832)
[1.] 31-I-2017, (1♂). [3.] 30-IV-2015, (1♂). [38.] 20-IV-2015, 1♂; 23-IV-2015, 1♂, 1 teneral ♀ (1♀). [40.] 20-IV-2015, (1♂). [48.] 22-IV-2015, (1♂). [55.] 17-XII-2013, 3♂♂ (1♂). [62.] 21-I-2017, 1♂.

Crocothemis sanguinolenta (Burmeister, 1839) (Fig. 45)
[7.] 28-I-2017, 1♂. [9.] 25-IV-2015, (1♂). [18.] 7-XII-2013, (2 ♂♂); 16-XII-2013, (1♂). [19.] 7-XII-2013, 2 ♂♂. [21.] 11-IV-2015, several individuals. [29.] 15-IV-2015, (1♂). [30.] 10-IV-2015, 3 ♂♂, 1♀ (1♂); 18-IV-2015, 1♂, 1♀. [31.] 11-XII-2013, (1♀). [43.] 20-IV-2015, (1♂).

Fig. 43. *Bradinopyga cornuta*, (A) male, (B) the wall of the old school with two settling ♂♂ (22-I-2017).

[48.] 22-IV-2015, 1♂. [51.] 9-XII-2013, (1♀) at the stream; 12-XII-2013, (1♀). [52.] 25-I-2017, (2 ♂♂) in the seepage-streamlet zone. [55.] 17-XII-2013, (1♀).

Fig. 44. *Crocothemis divisa*, **male (22-IV-2015).**

Fig. 45. *Crocothemis sanguinolenta*, **male (18-IV-2015).**

Fig. 46. *Diplacodes deminuta*, **male (25-I-2017).**

Diplacodes deminuta Lieftinck, 1969 (Fig. 46)

[1.] 31-I-2017, several ♂♂ (2♂♂). [24.] 23-I-2017, (1♂). [37.] 23-I-2017, (1♂). [38.] 27-IV-2015, (1 teneral ♂). [52.] 25-I-2017, 1♂ (phot.) in the seepage-streamlet zone.

Diplacodes lefebvrii (Rambur, 1842)

[1.] 31-I-2017, several ♂♂ (1♂), less numerous than *D. deminuta*. [31.] 13-IV-2015, (1♂); 16-IV-2015, (1♀). [59.] 15-XII-2013, 3♂♂ (1♂) at a bare seepage puddle on the riverbed margin. [65.] 13-I-2017, several ♂♂ (1♂).

Diplacodes luminans (Karsch, 1893) (Fig. 47)

[1.] 31-I-2017, numerous individuals. [3.] 30-IV-2015, (1 teneral ♂). [4.] 5-XII-2013, (1♀). [35.] 14-XII-2013, (1♂); 16-XII-2013, 2♂♂ at the both pond and stream; 18-XII-2013, 4♂♂ at the pond. [37.] 23-I-2017, numerous individuals mainly at the unused overgrown and drying up ponds. [38.] 23-IV-2015, (1 teneral ♂); 27-IV-2015, 1 teneral individual; 29-IV-2015, emergence, teneral individuals; 16-I-2017, very numerous, 7♂♂ at the small pool and 3♂♂ at the adjacent streamlet; 29-I-2017, numerous individuals. [39.] 16-I-2017, several individuals. [40.] 27-IV-2015, 1 teneral individual; 16-I-2017, 4 ♂♂. [44.] 17-I-2017, 1♂. [46.] 17-I-2017, 1♂. [47.] 17-I-2017, 2 ♂♂. [48.] 22-IV-2015, (1 teneral ♀); 17-I-2017, numerous individuals. [49.] 19-XII-2013, 1♂; 29-I-2017, numerous individuals. [52.] 25-I-2017, 2♂♂ in the seepage-streamlet zone. [55.] 17-XII-2013, 1♂. [56.] 10-XII-2013, (1♂) at the river pool. [58.] 8-XII-2013, 1♂, 1♀ (1♀). [59.] 15-XII-2013, (1♂). [60.] 24-I-2017, 2 ♂♂. [62.] 21-I-2017, 1♂. [65.] 13-I-2017, at least 6 ♂♂. [66.] 13-I-2017, 1♂.

Fig. 47. *Diplacodes luminans*, male (18-XII-2013).

Diplacodes pumila Dijkstra, 2006
[37.] 23-I-2017, (1♀).

Hemistigma albipunctum (Rambur, 1842)
[65.] 13-I-2017, (1♂, 1♀).

Nesciothemis farinosa (Förster, 1898)
[2.] 5-XII-2013, (1♂). [18.] 7-XII-2013, 3♂♂ (1♂); 20-I-2017, 1♂. [19.] 7-XII-2013, 3 ♂♂, one tandem in copula (2 ♂♂). [23.] 23-I-2017, 1♂. [27.] 14-XII-2013, 2 territorial ♂♂. [31.] 22-I-2017, 1♂, 1♀ (1♀). [33.] 14-XII-2013, 1 territorial ♂. [35.] 16-XII-2013, 1♂ (allochthonous?). [37.] 30-I-2017, 1 tandem in copula and then an ovipositing ♀. [43.] 17-I-2017, (1♂). [47.] 17-I-2017, 1♂. [48.] 17-I-2017, 1♂. [51.] 9-XII-2013, 9♂♂ at the stream (3 ♂♂, one of them teneral and one immature). [52.] 25-I-2017, several ♂♂ in the seepage-streamlet zone. [55.] 17-XII-2013, co-dominant, numerous ♂♂. [56.] 10-XII-2013, 1♂ at the river pool. [57.] 10-XII-2013, 1♂. [59.] 15-XII-2013, 1♂. [61.] 21-I-2017, 3♂♂ (1♂).

Notiothemis jonesi Ris, 1919 *
[7.] 27-I-2017, 3 territorial ♂♂ and 1 tandem in copula; 28-I-2017, 1 territorial ♂. All at stream pools. [11.] 26-I-2017, 2 territorial ♂♂ at a stream pool (1♂). [17.] 19-I-2017, 2♂♂ at a pool: an aggressive resident and a visiting intruder; 20-I-2017, 1 territorial ♂ (1♂).

Olpogastra lugubris Karsch, 1895 (Fig. 48)
[19.] 7-XII-2013, 1♂. [27.] 14-XII-2013, (1♂). [28.] 6-XII-2013, 2 individuals (1♂); 13-XII-2013, 1♂. [30.] 13-XII-2013, 1 individual. [33.] 14-XII-2013, 1 individual. [48.] 17-I-2017, 1♂. [55.] 17-XII-2013, 2♂♂ (1♂). [56.] 10-XII-2013, 1 tandem. [59.] 19-XII-2013, at least three ♂♂. [61.] 21-I-2017, 1 individual. [62.] 21-I-2017, 1♂.

Fig. 48. *Olpogastra lugubris*, male (19-XII-2013).

Orthetrum abbotti Calvert, 1892
[10.] 28-IV-2015, (1♂). [32.] 22-I-2017, 1♂, 1♀ and 1 tandem in copula. [33.] 13-IV-2015, (2 ♂♂, including 1 teneral); 22-I-2017, (1♂). [35.] 16-XII-2013, (1♂) at the pond; 18-I-2017,

1♀. [37.] 30-I-2017, 1♂, 1♀ in a spider's web. [51.] 9-XII-2013, several individuals, also immature, at the stream (2 ♂♂, 1♀); 12-XII-2013, 4 individuals (3 ♂♂) in the seepage-streamlet zone; 16-IV-2015, dominant in the seepage-streamlet zone, at least 20♂♂ and 2 copulations (1♂). [52.] 25-I-2017, (1♂) in the seepage-streamlet zone. [53.] 12-XII-2013, (1♀). [66.] 13-I-2017, (1♂).

Orthetrum brachiale (Palisot de Beauvois, 1817)
[1.] 31-I-2017, (2 ♂♂). [3.] 30-IV-2015, (2 teneral ♂♂). [15.] 7-XII-2013, (1♂). [19.] 7-XII-2013, (2 ♂♂). [28.] 24-IV-2015, (1♂). [35.] 14-XII-2013, (4 ♂♂) mainly at the pond and at puddles in the streamlet bed; 23-IV-2015, (1 immature ♂). [38.] 20-IV-2015, (1 teneral ♂); 16-I-2017, 4 ♂♂, 2 tandems, copulations and ovipositions (1♂), at the both pool and streamlet above the pool; 17-I-2017, ♂♂ and 1♀, oviposition; 29-I-2017, 1♂. [39.] 16-I-2017, ♂♂. [40.] 16-I-2017, 1♂. [44.] 17-I-2017, 1♂. [45.] 17-I-2017, ♂♂ at grassy broader sections. [46.] 21-IV-2015, (1 teneral ♂); 17-I-2017, 1♂. [47.] 17-I-2017, 1♂. [49.] 19-XII-2013, (3 ♂♂). [51.] 9-XII-2013, (4 ♂♂) at the stream. [60.] 21-I-2017, (1♂). [65.] 13-I-2017, (1♂).

Orthetrum chrysostigma (Burmeister, 1839)
[28.] 13-XII-2013, (1 teneral ♂); 24-IV-2015, numerous ♂♂ (3 ♂♂). [29.] 15-IV-2015, co-dominant, numerous ♂♂ (3 ♂♂). [31.] 12-IV-2015, (1♂). [33.] 13-IV-2015, (1♂). [44.] 21-IV-2015, (1 juvenile ♂). [47.] 17-I-2017, 1 tandem in copula (1♂, 1♀). [52.] 25-I-2017, 1♂ and 1 tandem (2 ♂♂, 1♀) in the seepage-streamlet zone. [53.] 12-XII-2013, (2 ♂♂). [55.] 17-XII-2013, (1♂). [56.] 10-XII-2013, numerous (5♂♂ shot down onto the water surface by children with the use of Phragmites-stems).

Orthetrum guineense Ris, 1910
[19.] 7-XII-2013, (1♂). [30.] 13-XII-2013, (1♂). [33.] 14-XII-2013, (1 teneral ♂).

Orthetrum hintzi Schmidt, 1951
[35.] 14-XII-2013, (1♀); 17-IV-2015, (1♂) at the flooded streamlet. [51.] 9-XII-2013, 2♂♂ (1 teneral) and 1♀ at the stream (2♂♂).

Orthetrum julia Kirby, 1900 (ssp. *falsum*)
[7.] 26-I-2017, numerous individuals, mainly ♂♂ (2 ♂♂); 28-I-2017, ♂♂. [8.] 28-IV-2015, 2♂♂ (1♂). [9.] 25-IV-2015, fairly numerous ♂♂ (1♂); 28-IV-2015, (2 ♂♂). [11.] 26-I-2017, (1 teneral ♂). [12.] 25-IV-2015, (1♂). [14.] 20-I-2017, 2♂♂ (1♂). [16.] 19-IV-2015, 4♂♂ (3 ♂♂). [18.] 20-I-2017, 1♂. [19.] 7-XII-2013, (1 teneral ♂). [20.] 11-IV-2015, (1♂). [21.] 11-IV-2015, several ♂♂ (1♂). [30.] 14-IV-2015, (2 ♂♂). [33.] 13-IV-2015, (2 ♂♂, including 1 immature). [36.] 18-I-2017, 1♂. [51.] 9-XII-2013, (1 teneral ♂) at the stream; 23-IV-2015, 2♂♂ (1♂) at a streamlet-tributary. [53.] 12-XII-2013, (1♂). [66.] 13-I-2017, 2♂♂ (1♂).

Orthetrum machadoi Longfield, 1955
[31.] 22-I-2017, (1♂). [66.] 13-I-2017, very numerous (at least several dozen) ♂♂, tandems (4♂♂).

Palpopleura deceptor (Calvert, 1899)
[38.] 16-I-2017, 1♂; 17-I-2017, 1 resident ♂. [40.] 29-I-2017, (1♂). [46.] 17-I-2017, 2♂♂ and 1 ovipositing ♀ (1♂, 1♀). [48.] 22-IV-2015, (1 teneral ♂); 17-I-2017, 1♂. [49.] 19-XII-2013, (3 ♂♂); 29-I-2017, 1♂. [52.] 25-I-2017, (1♂) at small pools in the seepage-streamlet zone.

Palpopleura jucunda Rambur, 1842
[51.] 12-XII-2013, several individuals in the fenny stream valley (4♂♂, 2♀♀).

Palpopleura lucia (Drury, 1773)
[29.] 15-IV-2015, (2♂♂). [38.] 21-IV-2015, 1♂; 23-IV-2015, 1♂. [40.] 20-IV-2015, 2 resident ♂♂. [44.] 17-I-2017, 1♂.

Palpopleura portia (Drury, 1773)
[9.] 25-IV-2015, 1♂. [10.] 28-IV-2015, 1 resident ♂, 1♀; 26-I-2017, 1♂. [20.] 11-IV-2015, 2 resident ♂♂, 1♀ (1♂). [29.] 15-IV-2015, 1♂. [34.] 13-IV-2015, numerous individuals at the pool and on adjacent fields (1♂). [35.] 14-XII-2013, (1♂) at the pond; 16-XII-2013, 1 territorial ♂ at the pond, 1 tandem at a small streamlet pool; 10-IV-2015, 1♂; 17-IV-2015, 3–4♂♂ at the pond; 18-I-2017, 1♂. [44.] 21-IV-2015, (1♂). [51.] 9-XII-2013, several individuals, both ♂♂ and probable ♀♀ in the potentially flooded grassy stream valley (3 ♂♂); 12-XII-2013, 4♂♂ in the fenny stream valley (2 ♂♂). [52.] 25-I-2017, 3♂♂ in the seepage-streamlet zone (1♂). [53.] 12-XII-2013, (1♂).

Pantala flavescens (Fabricius, 1798)
[18.] 20-I-2017, 2 individuals and 1 ovipositing tandem. [24.] 23-I-2017, 1 individual. [27.] 14-XII-2013, 1 patrolling ♂. [28.] 6-XII-2013, (1♀). [30.] 11-XII-2013, at first, very numerous foraging individuals and then, just before twilight, mass one-way migration. [32.] 22-I-2017, 1 foraging individual. [38.] 16-I-2017, 1 patrolling ♂, 1♀ and 1 ovipositing tandem; 17-I-2017, 1♂; 29-I-2017, 1 individual. [40.] 16-I-2017, 1♂. [41.] 16-I-2017, 2 ♂♂. [44.] 17-I-2017, 1♂. [45.] 17-I-2017, ♂♂ patrolling above the broader sections of the stream. [46.] 17-I-2017, 1 individual. [47.] 17-I-2017, 2 ♂♂. [48.] 17-I-2017, 2 ♂♂. [49.] 19-XII-2013, 1 tandem (1♂, 1♀); 29-I-2017, 1 patrolling ♂ and 1 teneral ♀. [52.] 25-I-2017, 1 individual in the seepage-streamlet zone. [55.] 17-XII-2013, 1♂. [56.] 10-XII-2013, numerous individuals at the broader section – the river pool. [57.] 10-XII-2013, 1♂. [58.] 8-XII-2013, fairly numerous individuals above a sandbar adjacent to a partly stagnant side arm of the river (1♀); 12-IV-2015, 1–2♂♂ at drying up pools – remains of the river flood. [64.] 12-I-2017, 3 foraging individuals. [65.] 13-I-2017, numerous individuals, both ♂♂ and ♀♀, 1 ovipositing tandem (1♂).

Rhyothemis semihyalina (Desjardins, 1832)
[64.] 12-I-2017, several individuals (2♂♂). [65.] 13-I-2017, 1♂.

Tetrathemis polleni (Selys, 1869) * (Fig. 49)
[60.] 21-I-2017, 3 territorial ♂♂, one of them also with a ♀ in copula (2♂♂).

Tholymis tillarga (Fabricius, 1798)
[3.] 30-IV-2015, (1 teneral ♀). [30.] 11-XII-2013, 1 foraging ♂ (crepuscular activity) (1♂); 10-IV-2015, several foraging individuals (1♀); 14-IV-2015, crepuscular activity, numerous foraging individuals – 7 ♀♀ and 1♂ in the checked sample (1♂); 23-IV-2015, numerous foraging individuals; 26-IV-2015, crepuscular activity, foraging individuals. [31.] 13-IV-2015, crepuscular activity, foraging individuals (1♂); 24-IV-2015, foraging individuals. [35.] 10-IV-2015, (1 foraging immature ♂). [61.] 24-I-2017, 1♂.

Tramea basilaris (Palisot de Beauvois, 1817)
[4.] 5-XII-2013, numerous individuals, probably foraging (3 ♂♂). [30.] 11-XII-2013, 2 foraging

Fig. 49. *Tetrathemis polleni*, male (21-I-2017).

individuals. [31.] 16-XII-2013, 1 individual; 22-I-2017, 1 foraging individual. [32.] 22-I-2017, 1 foraging individual. [35.] 16-XII-2013, 2♂♂ and 1 tandem at the pond (1♂). [37.] 23-I-2017, dominant at the used open pond: ♂♂ and tandems; 30-I-2017, 1♂. [38.] 16-I-2017, 1♂; 17-I-2017, 1–2♂♂ and 1 tandem; 29-I-2017, 1♂. [40.] 16-I-2017, 1♂; 29-I-2017, (1♂). [44.] 17-I-2017, 1♂. [46.] 17-I-2017, 1♂. [47.] 17-I-2017, 1♂. [48.] 17-I-2017, 2♂♂ and 1 tandem. [51.] 9-XII-2013, 1 foraging ♀. [53.] 12-XII-2013, (1♀). [57.] 10-XII-2013, 1 individual. [60.] 24-I-2017, 1 tandem. [61.] 24-I-2017, 1 individual. [64.] 12-I-2017, 2 foraging individuals. [65.] 13-I-2017, 1♂.

Tramea limbata (Desjardins, 1832) *
[1.] 31-I-2017, 1 patrolling ♂ and 1 tandem. [3.] 30-IV-2015, (1 patrolling ♂).

Trithemis aconita Lieftinck, 1969
[16.] 19-IV-2015, 1 tandem in copula (1♂). [18.] 7-XII-2013, (1♂). [28.] 24-IV-2015, (1♂). [35.] 16-XII-2013, (2 ♂♂); 18-XII-2013, 2♂♂ at the streamlet and streamlet pool. [45.] 17-I-2017, (1♂). [51.] 9-XII-2013, 1♂; 23-IV-2015, (2 ♂♂). [52.] 25-I-2017, 2♂♂ (1♂) in the seepage-streamlet zone. [55.] 17-XII-2013, (2 ♂♂).

Trithemis annulata (Palisot de Beauvois, 1807) (Fig. 50)
[55.] 17-XII-2013, 3♂♂ (1♂). [59.] 15-XII-2013, fairly numerous ♂♂ (3♂♂); 19-XII-2013, 1♂. [66.] 13-I-2017, 3♂♂ (2♂♂).

Trithemis arteriosa (Burmeister, 1839) (Fig. 51)
[1.] 31-I-2017, 1♂. [28.] 10-IV-2015, (3 ♂♂). [29.] 15-IV-2015, codominant, numerous ♂♂ (1♂). [35.] 14-XII-2013, (2 ♂♂); 16-XII-2013, 3♂♂ and 1♀ both at the pond and streamlet (1♂, 1♀); 18-I-2017, 6 ♂♂, mainly at the streamlet. [37.] 23-I-2017, several ♂♂; 30-I-

Fig. 50. *Trithemis annulata*, male (19-XII-2013).

Fig. 51. *Trithemis arteriosa*, male (17-XII-2013).

2017, numerous individuals, 2♂♂ in the spider web. [38.] 16-IV-2015, juvenile/immature individuals (1♂); 23-IV-2015, (1 teneral ♀); 29-IV-2015, 1 teneral ♂; 16-I-2017, 5♂♂ at

Fig. 52. *Trithemis donaldsoni*, male (17-XII-2013).

Fig. 53. *Trithemis pluvialis*, male (18-I-2017).

the streamlet above the pool. [45.] 17-I-2017, 2♂♂ (1♂). [46.] 17-I-2017, 1♂. [47.] 17-I-2017, several ♂♂. [48.] 22-IV-2015, 6 ♂♂, including 2 immature, at three broader stream

pools; 17-I-2017, 4 ♂♂, mostly at the broader stream pools. [51.] 9-XII-2013, (1 immature ♂) at the stream; 23-IV-2015, (1♂). [52.] 25-I-2017, fairly numerous ♂♂ in the seepage-streamlet zone. [53.] 12-XII-2013, (1♂). [55.] 17-XII-2013, codominant (1♂). [56.] 10-XII-2013, numerous ♂♂, at various sections of the river, both broader stagnant and narrower with rapids (4♂♂ shot down onto the water surface with the use of Phragmites-stems by children). [57.] 10-XII-2013, (1♂). [59.] 15-XII-2013, 2 ♂♂. [63.] 5-XII-2013, 1♂. [65.] 13-I-2017, 2♂♂ (1♂). [66.] 13-I-2017, 2♂♂ (1♂).

Trithemis donaldsoni (Calvert, 1899) * (Fig. 52)
[55.] 17-XII-2013, (3♂♂).

Trithemis furva Karsch, 1899
[16.] 19-IV-2015, (1♂) in a semi-open section with *Cyperus involucratus*. [21.] 11-IV-2015, 1♂.

Trithemis kirbyi Selys, 1891
[23.] 23-I-2017, 1♂. [29.] 15-IV-2015, numerous individuals, also tandems in copula (3 ♂♂). [36.] 14-XII-2013, (1 immature ♂). [45.] 17-I-2017, 3♂♂ (1♂). [46.] 17-I-2017, 1♂. [47.] 17-I-2017, 2 ♂♂. [48.] 22-IV-2015, 1♂; 17-I-2017, 3 ♂♂. [51.] 12-XII-2013, (1 teneral ♂). [52.] 25-I-2017, 1♂ in the seepage-streamlet zone. [56.] 10-XII-2013, fairly numerous ♂♂ (2 ♂♂). [58.] 12-IV-2015, 1♂ at drying up pools – remains of the river flood. [59.] 15-XII-2013, several ♂♂ at a stony seepage puddle on the riverbed margin (1♂).

Trithemis nuptialis Karsch, 1894 *
[66.] 13-I-2017, several ♂♂ and 1 tandem (2♂♂).

Trithemis pluvialis Förster, 1906 (Fig. 53)
[19.] 7-XII-2013, (1♂). [21.] 11-IV-2015, ♂♂ and 1 tandem in copula. [24.] 23-I-2017, several individuals (1 immature ♂). [28.] 24-IV-2015, 3♂♂ (1♂). [29.] 15-IV-2015, 3♂♂ (1♂). [33.] 13-IV-2015, (4 ♂♂). [35.] 16-XII-2013, (1♂) at the pond; 18-I-2017, 1♂; both probably allochthonous and attracted by a temporary streamlet [51.] 9-XII-2013, several individuals, both ♂♂ and ♀♀, at the stream (2 ♂♂, one of them immature, and 2♀♀). [52.] 25-I-2017, 1♂ in the seepage-streamlet zone. [53.] 12-XII-2013, (1♂). [56.] 10-XII-2013, 2♂♂ (1♂). [57.] 10-XII-2013, (1♂).

Trithemis stictica (Burmeister, 1839)
[2.] 5-XII-2013, (1♂).

Trithemis werneri Ris, 1912 * (Fig. 54)
[61.] 21-I-2017, several ♂♂ (3♂♂, two immature); 24-I-2017, in moderate numbers, dispersed at several sites.

Urothemis assignata (Selys, 1872)
[59.] 15-XII-2013, (1♂).

Urothemis edwardsii (Selys, 1849)
[56.] 10-XII-2013, 3–4 ♂♂ at the broader stagnant section – the river pool (1♂). [65.] 13-I-2017, (3♂♂, 1♀).

Fig. 54. *Trithemis werneri***, male (24-I-2017).**

Zygonoides fuelleborni (Grünberg, 1902)

[28.] 6-XII-2013, (1♂). [31.] 18-I-2017, (1♂). [55.] 17-XII-2013, 1 ExM, 1 ExF. [56.] 10-XII-2013, 1 ExM. [57.] 10-XII-2013, 3 exuviae (1 ExF). [59.] 19-XII-2013, 3♂♂ (1♂). [61.] 21-I-2017, (1♂); 24-I-2017, several individuals (1♂).

Zygonyx natalensis (Martin, 1900)

[14.] 20-I-2017, 1 tandem (1♂, 1♀). [16.] 20-I-2017, 1 patrolling ♂. [18.] 19-I-2017, 1♂; 20-I-2017, 1♂. [22.] 23-I-2017, 1 patrolling ♂. [23.] 23-I-2017, 1♂. [24.] 23-I-2017, 1 foraging ♀. [25.] 23-I-2017, 1 patrolling ♂. [29.] 15-IV-2015, 1♂ and 1 ovipositing tandem (1♀); 26-IV-2015, (1♂). [30.] 14-IV-2015, 7–8 foraging individuals (1♂); 15-I-2017, 1♂. [31.] 12-IV-2015, (1♂ foraging).

Zygonyx torridus (Kirby, 1889)

[6.] 5-XII-2013, 2♂♂ (1♂). [16.] 7-XII-2013, 2♂♂ (1♂). [18.] 20-I-2017, 2 ♂♂. [19.] 16-XII-2013, dominant, numerous ♂♂ and 2 tandems. [21.] 11-IV-2015, 2–3 ♂♂. [25.] 23-I-2017, 1♂. [27.] 14-XII-2013, 2♂♂ (1♂). [28.] 6-XII-2013, (1♂); 24-IV-2015, numerous ♂♂. [29.] 15-IV-2015, numerous ♂♂ and tandems, also ovipositing (1♂, 1♀). [30.] 6-XII-2013, (1 foraging ♂); 11-XII-2013, 1 foraging individual. [32.] 22-I-2017, 1 foraging individual. [43.] 17-I-2017, 1♂. [45.] 17-I-2017, 3 ♂♂. [47.] 17-I-2017, 2 individuals (including 1♂). [48.] 17-I-2017, 1♂. [52.] 25-I-2017, 3♂♂ in the seepage-streamlet zone. [53.] 12-XII-2013, 1 tandem (1♂, 1♀). [55.] 17-XII-2013, 3♂♂ (1♂). [56.] 10-XII-2013, 2♂♂ and 1 ovipositing ♀ (1♂).

Species richness and frequency

Collecting 104 species in the relatively small study area was achieved due to thorough research based on many controls repeated at the same water bodies in various phases of the rainy season – from its very beginning, through its peak, up to the very end. However, the number of recorded species would certainly have been higher if more water bodies had been studied, especially in hardly accessible dambos on the plateau and the inaccessible wet mountain valley of the upper Chingombe River.

The species composition and relative richness was a consequence of the close proximity of three quite different geomorphological and hydrological units: a) undulated uplands rich in seasonally wet dambos, b) steep escarpment slopes with mountain watercourses, and c) the flat bottom of the rift valley joining submontane permanent watercourses, a fairly large river and temporary waters. The diversity affecting dragonflies and damselflies also included local climatic conditions, ranging from humid subtropical in upper elevations to tropical savanna in lower ones. As a result, several interpenetrating odonate assemblages co-occurred in a small area, and *Chlorocypha consueta*, finding optimum in shaded highland streams, or *Allocnemis marshalli*, preferring mountainous seepages and small streams, literally almost met *Pseudagrion commoniae* or *Orthetrum chrysostigma*, both restricted to the hot and open tropical valley.

We could assess only the relative frequency of species in the Chingombe area. For each species, it was understood as a percentage of recorded localities in the total number of 62 studied localities. Some species might have been allochthonous at some localities – only as guests from other localities nearby. This was especially obvious for a few localities without water habitats, thus 'collecting' dragonflies from their environs. However, even such a rough and fuzzy picture to some extent reflected the actual proportions between species in the study area. About one-fifth of the odonate fauna, i.e. 21 species, was assessed as relatively fairly frequent to frequent species (17.7–33.9%, 11–21 localities) in the study area (Table 1).

Table 1. Number of localities (No.) and relative frequency (%) of relatively fairly frequent to frequent odonate species in the environs of Chingombe, central Zambia.

Species	No.	%
Pseudagrion kersteni	21	33.9
Diplacodes luminans	20	32.3
Pantala flavescens	20	32.3
Nesciothemis farinosa	19	30.6
Zygonyx torridus	19	30.6
Tramea basilaris	17	27.4
Trithemis arteriosa	17	27.4
Elattoneura glauca	16	25.8
Orthetrum brachiale	16	25.8
Orthetrum julia	16	25.8
Phaon iridipennis	16	25.8
Chlorocypha consueta	14	22.6
Crocothemis sanguinolenta	13	21.0
Gomphidia quarrei	13	21.0
Platycypha caligata	13	21.0
Pseudagrion hamoni	12	19.4
Pseudagrion sublacteum	12	19.4
Trithemis kirbyi	12	19.4
Trithemis pluvialis	12	19.4
Olpogastra lugubris	11	17.7
Pseudagrion hageni	11	17.7

The next 21 species were perceived as occurring with moderate frequency (9.7–16.1%, 6–10 localities). As is typical of many faunas, the largest (62 species) was the category of the least frequent species, i.e. these uncommon and rare (1.6–8.1%, 1–5 localities) in the Chingombe area; half of them were recorded only at one locality.

Odonate fauna of habitats

The species composition and relative frequencies of species largely reflected the frequency of particular habitats combined with local climatic conditions. It must be stressed that the habitat spectrum was based on stronger permanent watercourses and temporary waters with a total lack of permanent standing waters. This lack was followed by the total absence or only scarce occurrence of widespread and elsewhere common species that are related to more perennial still waters. Rare *Ischnura senegalensis*, *Anax imperator* and *Urothemis edwardsii*, occasionally recorded at broad and stagnant stream/river pools, seemed to be only a minimal representation of this group of species.

Permanent watercourses were represented by three general types: a) mountain and plateau streams, situated above 600 m a.s.l. (locally descending to 580 m), b) submontane streams and small rivers flowing at the bottom of the rift valley, i.e. below 600 m a.s.l., and c) a fairly large river being a longitudinal axis of the rift valley.

Mountain and plateau streams

Nine species were recorded exclusively at upland (mountain and plateau) streams: eight of them (*Allocnemis marshalli*, *Elattoneura cellularis*, *Pseudagrion spernatum*, *Heliaeschna fuliginosa*, *Notogomphus* cf. *zernyi*, *Phyllomacromia monoceros*, *Notiothemis jonesi* and *Trithemis furva*) only in the mountains and one (*Trithemis stictica*) only on the plateau. Additionally, *Chlorocypha consueta* was almost totally restricted to these upland habitats. Outside this zone, it was found only in very small numbers at one locality at the bottom of the rift valley, i.e. at the Bwingi Stream, which corresponded to mountain watercourses, due to its shading and seepage feeding (Fig. 22). Two other species, *Pseudagrion hageni* and *Orthetrum julia*, also occurred more frequently at the upland streams than at the watercourses at the bottom of the rift valley.

We investigated a typical mountain watercourse, the Mikwa stream system, from its source (1180 m a.s.l.) down to its mouth into the Chingombe River (560 m a.s.l.), the lowest place situated already at the bottom of the rift valley (Fig. 1). Fifteen localities studied in the mountainous zone mostly included the main stream, but also its small tributaries, adjacent seepages and small stream-dependent pools (Figs 9–12). Clear differences between its upper reaches (above 1000 m a.s.l., loc. 7–12) and lower reaches (below 700 m. a.s.l., loc. 13–21) were noticed. The upper reaches of the stream were mostly narrow and shaded, but highly heterogenous morphologically, with diverse microhabitats of stronger-current sections and calmer stream pools, and with correspondingly different bottom deposits (Figs 9, 10). It was also accompanied by small tributaries, trickles and seepages. The lower reaches of the stream still retained their mountainous nature (Fig. 12), but were wider, more homogenous morphologically and generally stronger, shaded with several sunny glades and clearings,

and fed by less frequent accompanying waters. These habitat differences were reflected in the odonate assemblages. Three species, *Heliaeschna fuliginosa, Phyllomacromia mono-ceros* and *Pseudagrion spernatum*, were only recorded in the uppermost section of the stream, where *H. fuliginosa* apparently selected the stream micropools. The clear attachment of *Notiothemis jonesi* to the small stream pools was also decisive for its almost exclusive occurrence in the upper reaches, as was the case with *Allocnemis marshalli*, so relating to trickles and seepages. The upper reaches also seemed to be an optimum habitat for *Chloro-cypha consueta* which was far less numerous in the lower reaches. In contrast, *Platycypha caligata* was restricted in the stream only to its lower reaches, where it occurred regularly. A second similar pair of counterparts included *Elattoneura cellularis* and *E. glauca*. While the former was almost totally restricted to the upper reaches of the stream, the latter occurred almost exclusively in its lower reaches as well as at the adjacent bottom of the rift valley. Two species, *Notogomphus* cf *zernyi* and *Trithemis furva*, were rarely recorded only in the lower reaches of the Mikwa stream, the latter occurred only in sunny glades.

Submontane permanent streams and small rivers at the bottom of the rift valley

The smaller permanent watercourses in the valley were perennial mostly due to its moun-tain/plateau origin, thus their flow and level were variable and partly related to the upland rainfall: the lowest at the end of the dry season and the highest in the peak of the rainy season. Contrary to the mountain and plateau watercourses, most of them were semi-open to open and partly to strongly insolated, thus really tropical in their nature. They were mostly flanked by vegetation, especially by high *Phragmites mauritianus*, and partly diversified be-tween broader calm sections and shallow rapids (Figs 15, 22–24).

Only two watercourses, the Bwingi stream (loc. 51–52) and a nameless stream (loc. 53), were born at the bottom of the rift valley, just at the foot of the escarpment, the former in a large seepage area and the latter in hot springs. The Bwingi Stream differed from other low-elevated streams by (a) the extensive seepage zone, (b) the broad, fenny valley and (c) the main watercourse morphologically strongly diversified and largely shaded (Fig. 22).

The odonate fauna of permanent submontane streams and small rivers was rich, but much less specific than that of the mountain and plateau watercourses. Apart from the rare *Lestino-gomphus angustus* and *Trithemis donaldsoni*, we did not find any species clearly restricted to them. The former was recorded at two watercourses locally shaded by low trees and shrubs and the latter was evidently related to a specific combination of abundant boulders and strong insolation unique in this plane area. Except for a female of unknown origin, the next rare species, *Paragomphus sabicus*, seemed to have also been associated with the unique conditions provided by one of the valley watercourses, i.e. the tropical Bwingi stream shaded by the gallery forest. Generally, however, most species inhabiting smaller permanent watercourses in the valley also occurred in other habitat types with common features. For example, *Pseudagrion sublacteum* and *Orthetrum chrysostigma* were also recorded at a temporary stream and many species also occurred by flowing mountain waters and/or a large river.

The group joining the valley's smaller watercourses and lower reaches of mountain streams and rivers was especially rich. This generally included species of open and semi-open land-

scapes, which also used forest glades, clearings or places with shade and light mosaic, such as *Elattoneura glauca*, *Platycypha caligata*, *Crenigomphus hartmanni*, *Trithemis pluvialis*, *Nesciothemis farinosa*, *Gomphidia quarrei*, and even *Ictinogomphus ferox* typical of broader and calmer sections.

Species occupying the opposite side of this continuum, such as *Olpogastra lugubris* and *Zygonoides fuelleborni*, occurred in both the valley's smaller watercourses and the large river. The highly variable form and conditions of this large river might have facilitated the occurrence in seemingly different habitats. In fact, the Lukusashi River offered quite similar conditions to smaller watercourses during a large part of the year, as it was divided into anastomosing and partly very shallow branches (Fig. 25) within the dry period and first weeks of the rainy period.

Large river

The occurrence of three other species, *Brachythemis lacustris*, *Mesocnemis singularis* and *Pseudagrion acaciae*, also covered the valley's smaller watercourses and the large river, but appeared to be more centred on the latter. For example, the first species was abundant at the large river and only sparse at open lower reaches of its some smaller tributaries.

Five further species, *Mastigogomphus* cf. *dissimilis*, *Brachythemis leucosticta*, *Pseudagrion glaucescens*, *Ceriagrion kordofanicum* and *Trithemis werneri* were recorded only at the large river. In the low water phase, four former species were associated with side, calmer and even partly stagnant arms of the river, partly separated from the main course by barren sand- and gravel bars (Fig. 25). Relation of *C. kordofanicum* to the large river was driven by *Pistia* floating along the margins of these arms; it was the only one habitat where this plant species occurred in the study area.

Temporary waters in the rift valley

Temporary waters at the bottom of the rift valley were represented by various pools, puddles, inundated sites and watercourses. At least six species were recorded only in these types of valley habitats: *Lestes ictericus*, *Ceriagrion mourae*, *Ceriagrion suave*, *Crocothemis divisa*, *Palpopleura deceptor* and *Tetrathemis polleni*.

The most extensive and most intensively studied example of these waters was the Mulembwe Stream, a temporary watercourse with many broader sections forming small stream pools. The stream was flowing between the first phase of the rainy season (December/January) and the first month of the dry season (April or May), making at least four months. However, the stream pools must have remained longer, with some of them even remaining much longer in the wettest years. Generally, the stream flowed weakly in an open grassy corridor between dry miombo woodlands (Fig. 19A). Its shallow bed was not well-demarcated, so shallow flooding occurred locally (Fig. 19B). In many places, it was rich in stones and small boulders producing small riffles. The stream pools were partly to totally overgrown by vegetation, especially by grasses, and they were generally strongly insolated with some shaded sites (Figs 17, 18, 20).

The odonate fauna of this stream-complex was rich: 33 species were recorded and two of these, *Ceriagrion mourae* and *C. suave*, were found only there. Although dragonflies and damselflies occurred alongside narrow sections, they evidently concentrated at stream pools, which were responsible for the species abundance and richness. Species well adapted to temporary waters formed the core of the assemblage. In the first place, this group included such temporary water specialists as *Lestes ictericus*, *Ceriagrion banditum*, *Ceriagrion mourae*, *Ceriagrion suave*, *Anax ephippiger*, *Anax tristis*, *Palpopleura deceptor* and *Pantala flavescens* – all of which were associated with stream pools. They were accompanied by at least 15 species often inhabiting temporary waters, such as e.g. *Agriocnemis exilis*, *Pseudagrion commoniae*, *Pseudagrion hamoni*, *Paragomphus genei*, *Diplacodes deminuta*, *Diplacodes luminans*, *Orthetrum brachiale*, *Tramea basilaris* and *Trithemis kirbyi*. However, several species less related or unrelated to temporary waters were also recorded at Mulembwe Stream. While *Pseudagrion sublacteum* and *Orthetrum chrysostigma* certainly locally developed in the stream-complex, the native occurrence of some other species (*Nesciothemis farinosa*, *Zygonyx torridus*) appeared uncertain, despite several males being recorded. Some of the possibly non-native species might simply have been attracted by the distinguishing proximal cues of their typical habitats, such as stones (*Crocothemis sanguinolenta*), shade (*Trithemis aconita*) or riffles (*Zygonyx torridus*). The odonate fauna was completed by certainly allochthonous species, i.e. very rare vagrants from permanent watercourses, such as *Olpogastra lugubris* and *Anax speratus*.

Two small clayey pools in a strongly eroded ravine (channelling waters after heavy rains to the nearby large river) were a specific type of temporary waters. With their soft clayey bottom, turbid yellowish water and overhanging branches (Fig. 26), they met the requirements of *Tetrathemis polleni*, a spectacular species found nowhere else in the study area.

Broadly flooded, great, deep and bare road puddles attracted a few species typical of temporary waters, such as *Paragomphus genei*, *Anax tristis*, *Pantala flavescens* and *Pseudagrion hamoni*. The behaviour of individuals and the long existence of these water bodies suggested the possibility of successful breeding there, but we could not confirm these expectations during too short an expedition.

Temporary waters on the plateau

Temporary waters on the upland plateau were represented by numerous water bodies in dambos, i.e. river-like open valleys flanked by miombo woodlands. We only studied two examples of this habitat, so it is impossible to describe it reliably. However, even those results provided distinguishing features and thus were noteworthy.

Temporary water bodies in dambos were generally larger, deeper and more stable in comparison with the temporary waters at the bottom of the rift valley (Figs 6, 8). They existed not only during the wet season, but also in the subsequent cool phase of the dry season, i.e. between January and July/August. The Dambo Kabufumu was still partly inundated with water in the second half of August, i.e. more than three months after the end of the rainy season, but before the hottest and driest months of the year. Even the semi-permanent nature of some these water bodies could not be excluded in the wettest years, as vegetation in Dambo Kabasa suggested in 2015. Much richer and structurally more hetero-

genous water vegetation (Figs 6, 8), in comparison with the monotonous temporary waters at the bottom of the rift valley, was another important factor certainly influencing the local odonate fauna.

The dambo habitats that were studied were dominated (80% out of 27 recorded species) by dragonflies and damselflies mostly or at least often occurring in temporary waters. As many as nine species (*Lestes amicus*, *L. dissimulans, L. virgatus*, *Aciagrion africanum*, *Aethiothemis bequaerti, A. solitaria, Acisoma inflatum*, *Tramea limbata* and *Gynacantha manderica*) were recorded only in dambos. This quite high specificity probably resulted from a combination of more favourable habitat conditions and milder mesoclimate between wooded slopes at 1200 m a.s.l. in comparison to the tropical and drier bottom of the rift valley, 600–800 m below.

Proximal cues

Some odonate species are frequently associated with proximal cues of their habitats, i.e. with particular morphological elements or traits detected visually and used specifically. These elements may shape ultimate factors, i.e. key habitat conditions, and/or inform about their occurrence (Sternberg 1999). In the study area, the species composition might have been affected by the proximal cues determining the occurrence, abundance and behaviour of some species (Table 2).

Stones and boulders exposed in or alongside the water were a diagnostic feature of habitats used by several *Trithemis*- and *Crocothemis*-species (Table 2). *Crocothemis divisa* was restricted to two savannah temporary streams, flowing between grass and scattered stones (Figs. 19, 20) – substrate used by settling males (Fig. 44). *Trithemis kirbyi* was much less selective using stony substrates on both temporary and permanent watercourses of various size, from narrow streams to the large river. A kind of stone-based spatial segregation even occurred between *T. kirbyi* and coexisting congeners, *T. arteriosa* and *T. pluvialis*, at the broad road ford on the Chingombe River. Numerous males of the former were very active there: they spent most of their time in flight above the water table and settled exclusively on stones on the riverbanks or on the logs of the footbridge, but never on vegetation and never in close proximity to males of other *Trithemis*-species. Males of the two latter species behaved like typical perchers: they mostly occupied the riverbanks, perching on stems of herbaceous plants, even in close proximity to each other, but not to *T. kirbyi*.

The Mikwa Stream abounding in stones and boulders was a favourable habitat for *C. sanguinolenta*. especially in its lower reaches with sunny clearings. However, the species was also recorded at the Bwingi Stream, which is almost devoid of stones. The many exposed large tree roots crossing the stream bed might have been a sufficient substitute of stones there. Settling *C. sanguinolenta* also used related anthropogenic structures such as a stony wall (Fig. 45) in the vicinity of the power station canal flowing in the concrete bed. Another species using man-made structures was *Bradinopyga cornuta*, naturally associated with rocks, but in the study area only to an old, damaged school. Its intricate colour pattern did not match red brick, but five males "made a mistake" by persistently settling on the brick wall (Fig. 43). They were probably attracted by the concrete and stony puddles collecting roof rainwater around the school walls.

Table 2. Selected habitat proximal cues affecting species occurrence, recorded in the present study in central Zambia, with references to earlier literature sources.

Species	Proximal cues	Reference to the representative literature
Crocothemis divisa Crocothemis sanguinolenta Trithemis donaldsoni Trithemis kirbyi	Stones and boulders	Suhling & Martens (2007); Tarboton & Tarboton (2019)
Bradinopyga cornuta	Brick wall as an equivalent of rocks	Dijkstra & Clausnitzer (2014)
Phaon iridipennis Pseudagrion hageni Heliaeschna fuliginosa Phyllomacromia monoceros Notiothemis jonesi Trithemis aconita	Shade	Suhling & Martens (2007); Dijkstra & Clausnitzer (2014); Tarboton & Tarboton (2019); Dijkstra (2021)
Tetrathemis polleni	Branches over-hanging turbid water	McCrae & Corbet (1982); Dijkstra (2021);
Zygonyx torridus	Rapids and riffles	Suhling & Martens (2007); Martens (2015); Dijkstra & Clausnitzer (2014)
Paragomphus genei	Bare ground adjacent to the water	Tarboton & Tarboton (2019)
Ceriagrion kordofanicum	Pistia rosettes	Dijkstra & Clausnitzer (2014); Dijkstra (2021)

All species clearly associated with shade (Table 2) occurred on permanent watercourses, mostly streams, but in *Phaon iridipennis* also small rivers. *Phaon iridipennis*, *Trithemis aconita* and *Pseudagrion hageni* were also recorded at one or two seasonal streams, but only in the last species did we observe tandems, submerged oviposition and tenerals, thus providing evidence of its native occurrence there.

The degree of habitat specialization in shade-seeking species was diverse. More specialized *Heliaeschna fuliginosa* and *Notiothemis jonesi* selected shaded calm micropools with a thick layer of detritus and leaf litter (Figs 10, 11, 13), situated on the run of the mountain streams and trickles feeding them. Less specialized *Phaon iridipennis*, *Trithemis aconita* and *Pseudagrion hageni* inhabited not only shady streams, but also the shaded banks of small half-open and open watercourses.

Several species were associated with shaded habitats, but in some situations at least they searched for direct sunshine. Males of *Phyllomacromia monoceros* rapidly patrolled the deeply shaded section of the mountain stream with calm micropools, but they also entered the sunny clearing and one of them foraged in full 'sun'. *Pseudagrion hageni* used the shade and light mosaic. *Chlorocypha consueta* and *Allocnemis marshalli*, in turn, settled in sunny microspots in a deeply shaded environment: the former species low on stones and fallen wood as well as higher on small branches, while the latter on leaves, even relatively high.

Heliaeschna fuliginosa, *Phyllomacromia monoceros* and *Notiothemis jonesi* were active in deep shade, but in sunny weather. This was highly symptomatic, when all males of N. jonesi appeared at shaded territorial sites exclusively in sunny moments and disappeared at cloudy times. Quite the opposite situation was observed twice in *Phaon iridipennis* in December, at the beginning of the wet season. In sunny weather, this species was really seldom seen out of deep shade, and thus was hardly detectable and certainly underestimated. However, in two localities, we observed several individuals being active in completely open places. Both these 'atypical' situations had common weather conditions: after rain (storm), with an overcast sky and at most subdued sunshine. Additionally, we were able to compare this overcast picture to 'typical' sunny conditions in exactly the same places, and the impression was striking: in both these localities, individuals of *P. iridipennis* seemed to be much more numerous, active and detectable in overcast than in sunny weather, due to the penetration of open sites. We interpreted this phenomenon as 'stepping out of the shade' stemming from much weaker insolation in open areas. However, in this weather, most other dragonfly species were largely absent from these places, or at least were much less active in comparison to sunny weather. Thus, more open activity of *P. iridipennis* might have been the combined effect of favourable light/temperature conditions and the weaker pressure of other odonates.

A slightly similar effect was once observed in *Pseudagrion gamblesi*. This species was seemingly not shade-loving, as it inhabited the open and semi-open sections of small rivers and large streams and visited directly insolated sites. However, individuals flying and settling above the water table were mostly observed under overhangs of high herbaceous vegetation, e.g. *Phragmites mauritianus*, or in proximity to them. Thus, we had some impression of shade-seeking behaviour in a generally open environment in almost all observations of the species apart from that made in after-rain conditions on the same day as in *P. iridipennis*. In the overcast weather with at most subdued sunshine, individuals of P. gamblesi seemed to be much more active and detectable in entirely open places without overhanging vegetation in comparison to 'typical' sunny situations. Increased activity in specific not sunny weather conditions was also noticed in gomphids (see next chapter).

Overhanging branches were a proximal cue corresponding to shade. Together with clayey, turbid water, they distinguished the habitat of *Tetrathemis polleni* (Fig. 26). Males of this species were certainly not shade-loving, as they perched in full tropical sunshine during the hottest hours. However, a copulating tandem 'dived' low under overhanging branches and after a moment, only the male flew out alone, settling again on its perch. It seems probable that the female oviposited in the shade, attaching eggs to small branches or sticks above the water table, as is known to be the case with this species (McCrae & Corbet 1982).

'Hiding' exposed eggs under dense, overhanging branches would thus save them from both potential ovivorous animals and the scorching sunshine.

'Gomphid day'

Adults of many tropical gomphids are elusive and furtive and encounters with them, especially with males, are incomparably rarer than finding their exuviae. This 'model' works in full in Africa (e.g. Dijkstra & Clausnitzer 2014) including central Zambia. Apart from *Ictinogomphus ferox* and *Gomphidia quarrei*, characterised by overt and aggressive behaviour, and ubiquitous *Paragomphus genei*, we observed gomphids only rarely and very briefly, in fact, elusively. We collected them exceptionally, and these tended to be tenerals and juveniles rather than adults.

Against this typical background, observations made on the 22nd of January (the peak of the wet season) appear to be extraordinarily rich and unique. In a small area at the Chingombe mission (loc. 31–33), out of water, we observed adults of five species during a short time: *Crenigomphus hartmanni*, *Gomphidia quarrei*, *Lestinogomphus angustus*, *Paragomphus cognatus* and *Paragomphus elpidius*. What is more, each species was also represented by a male or males. Observations of male *C. hartmanni* and *P. elpidius*, as well as *L. angustus* in tandem, were unique during our study in Zambia. It should be stressed that we visited these sites in the direct surroundings of our operating base many times during three expeditions but without any result. We also searched especially for gomphids in similar habitats elsewhere and on many occasions, yet we only met single adult gomphids out of water a couple of times. Apart from this unique concentration, the behaviour of gomphids was also unusual. They were not very active and were thus quite easily approachable. They mostly perched on higher herbaceous vegetation and lower bush twigs and when scared, they landed only several metres away. On this day, other dragonflies were also observed foraging or perching in these places, including the hanging and seemingly 'lazy' *Phyllomacromia picta*.

This concentration, along with the more 'open' and less shy behaviour, might have been related, directly or indirectly, to specific weather conditions. After night-time rainfall, the late morning and early afternoon of that 'gomphid day' were windy and warm, but not hot. It was cloudy at first, but later this combined with subdued sunshine coming through clouds and warming vegetation in sheltered places. These mild and more temperate weather conditions were also unique during our three expeditions, which were otherwise mostly dominated by clearly patterned weather: sunny and hot or cloudy and rainy, and almost never windy. We strongly recommend searching for gomphids in similar weather conditions in tropical Africa to confirm and analyse this phenomenon.

Phenology

Predictably, phenology of Odonata in the Chingombe area was generally driven by the wet season. However, the phenological rhythm of the odonate fauna differed significantly between temporary waters and perennial watercourses.

Temporary waters

In the temporary waters, phenology of odonate assemblages in the wet season was distinctly patterned, with two consecutive aspects dominated by reproductively active adults and emerging tenerals, respectively. At the beginning of the wet season, the reaction of adult odonates to first heavier rains was extremely rapid. We had the impression that damselflies and dragonflies were 'in the starting blocks', ready to react immediately to the first appearance of water and to colonise it. What is more, they appeared in potential habitats even before surface water. In the Dambo Kabufumu (loc. 1), neither the surface water nor Odonata were present on the 5th of December, at the very end of the dry season. On the 20th of December, after the first heavy rains (which had begun a week earlier), but still without water discernible on the ground surface (Fig. 6A), nine species were recorded in the area of the future pool, including seven damselfly species (*Lestes amicus*, *L. dissimulans, L. virgatus*, *Aciagrion africanum*, *Africallagma fractum*, *A. pallidulum*, *Ceriagrion banditum*), and two dragonfly species (*Anax ephippiger*, *A. tristis*). While dragonflies were still rare and rather temporarily present, damselflies were fairly numerous and clearly resident and even the reproductive behaviour of three species, *L. dissimulans*, *C. banditum* and *A. fractum* (in each case one tandem), was already observed. Another similar situation was observed in the valley of the Bwingi Stream (loc. 51), where *Africallagma pallidulum* was recorded in still dry grassy depressions from the 9th of December, thus even before the first heavy rains, but in increased numbers after them. Both males and females were very localised there, strictly restricted to a small area, where the vegetation structure suggested potential flooding. It seems that the terrain morphology and vegetation structure in both the Kabufumu and Bwingi valleys served as some proximal cues and as a waiting and shelter space for Zygoptera pending water in potentially favourable habitats.

Anisoptera, in turn, were rapid colonisers of habitats immediately after the appearance of surface water. On the 19th of December, after the heavy rains of the two previous days, a temporary pool (loc. 49) was still in statu nascendi: this was only a small (50 m^2) and very shallow puddle in comparison to its future fully filled size (Fig. 21). Despite its one-day-long existence and apparent non-attractiveness, a strong representation of Anisoptera was already present, with five species, territorial and aggressive males and even the first reproduction: *Pantala flavescens* (tandem), *Orthetrum brachiale* (3♂♂), *Palpopleura deceptor* (3♂♂), *Anax tristis* (2 consecutive ♂♂ and 1♀), and *Diplacodes luminans* (1♂). In contrast to the Dambo Kabufumu, Zygoptera were almost lacking and were represented solely by one unidentified female of *Lestes* sp. This poor representation was probably a consequence of still lacking vegetation that might have suggested a future pool and might have provided a space for reproduction and shelter.

A mass displacement of a classic example of temporary water species, *Pantala flavescens*, might have announced the approaching rainy season. On the 11th of December, two days before first the heavy rains, large numbers of individuals of this species – accompanied by rare *Tramea basilaris* – were observed in the late afternoon, before sunset. In the sultry and overcast, 'tense' weather, all these densely scattered individuals simultaneously flew at fairly great height in the same direction.

During the peak of the wet season (the second half of January), adult Odonata were still generally numerous and active at temporary waters. However, adults of several species (e.g.

Lestes ictericus, *Aciagrion africanum*, *Africallagma fractum*, *A. pallidulum*, *Ceriagrion suave*) were already not observed in the places where they had occurred (or must have occurred) at the beginning of the wet season. This lack suggested a generation gap of imagines and a partial time segregation of species. Emerging individuals, in turn, occurred only in two species, *Lestes ictericus* and *Agriocnemis exilis*. This was interpreted as the early beginnings of emergence of probably the most rapidly developing species as a consequence of the very early wet season that year: heavy rains had already started in November there.

In contrast to the first half of the wet season, the late phase of it was a distinctive time of emergence in temporary waters. Only teneral or juvenile individuals were observed at the temporary water bodies and nearby from many species more or less related to these habitats, e.g. *Lestes amicus*, *L. dissimulans*, *L. ictericus*, *L. virgatus*, *Ceriagrion banditum*, *C. mourae*, *C. suave*, *Diplacodes deminuta*, *D. luminans*, *Orthetrum brachiale* and *Palpopleura deceptor*. However, the assessed general intensity of emergence clearly decreased towards the very end of the rainy season. We did not observe any subsequent homing of mature individuals of e.g. *Ceriagrion mourae* and *C. suave* to their native stream pools on the Mulembwe Stream. Considering the already declining water conditions there, the emerged individuals of these temporary water specialists most probably returned for reproduction only 7–8 months later, at the beginning of the next wet season. The end of the reproductive activity of *C. mourae* recorded in the first half of the wet season might confirm such a scenario.

In the larger and much longer-lasting water body in the upland Dambo Kabasa, the odonate assemblage in the late wet season was similarly dominated by teneral and juvenile individuals. However, at least in *Aciagrion africanum* and *Ceriagrion glabrum*, tenerals occurred in parallel with adults and even reproductive activity of the former was possible. Due to much less limiting water conditions, time segregation of generations might have been less acute there in some species than in the smaller and shorter lasting water bodies at the bottom of the rift valley.

The occurrence of six species of Gynacanthini at the end of the wet season in April including five foraging species concentrated at one locality – suggested their phenological rhythm, which is typical of temporary waters, with the emergence in the late wet season and reproductive activity after many months in the first phase of the next wet season. This interpretation was strengthened by juvenile and teneral individuals of *Heliaeschna trinervulata* and *Gynacantha manderica* collected in April. Individuals from four other *Gynacantha*-species (*immaculifrons, vesiculata, villosa* and new undescribed species) might also have been juvenile/immature, as their faintly marked green colours suggested. The interpretation of the appearance of the four *Gynacantha*-species in the late wet season as a post-emergence phenomenon could also be supported by the emergence of *Gynacantha vesiculata* recorded in northern Nigeria exactly in the same phase of the wet season (Gambles 1960). In contrast to April's relative abundance of Gynacanthini in central Zambia, only one adult individual from one species was recorded at the same locality at the beginning of the wet season and no individuals were found there during the peak of it, despite several repeated controls focused on the search for these dragonflies.

Small permanent watercourses

In the smaller permanent watercourses, phenology of the odonate assemblages during the wet season was generally less patterned, without a dramatic change of generations and without any phenological aspect clearly dominated by emergence and juveniles. Emergence in the assemblages was more scattered in time and occurred in all phases of the rainy season. However, it was centred in the first half of it in contrast to temporary waters. This effect was partly due to several gomphids (*Crenigomphus hartmanni*, *Ictinogomphus ferox*, *Lestinogomphus angustus*, *Notogomphus* cf. *zernyi*, *Paragomphus sabicus*), whose emergence was recorded almost only in December, i.e. just before the start of the rainy season and at the beginning of it. However, a single emerging *Crenigomphus hartmanni* was recorded even in mid-April, near the end of the rainy season.

Gomphids, like some other species (e.g. *Nesciothemis farinosa* and *Olpogastra lugubris*), distinguished the early phase and height of the wet season and almost did not occur at all in the late phase of it. In contrast, some other species appeared to be flourishing, especially at the peak of the rainy season (e.g. *Allocnemis marshalli*, *Notiothemis jonesi*) or at the height and at the end of it (e.g. *Chlorocypha consueta* and *Orthetrum julia*), though at least the two latter were continuously represented by adults at the watercourses during the wet season. What is more, at least seven species (*Platycypha caligata*, *Chlorocypha consueta*, *Phaon iridipennis*, *Crocothemis sanguinolenta*, *Orthetrum julia*, *Trithemis pluvialis* and *Zygonyx natalensis*) were also recorded during the peak of the dry season between August 20th – 23rd, during the reconnaissance at the permanent Mikwa Stream in 2011 (Daraż 2013).

As an effect of replacing individuals and the prolonged occurrence of many species, the odonate assemblages of small permanent watercourses appeared more stable and continuous than those of temporary waters, although they were richer in the first half of the rainy season. This phenological characteristic was a function of quite stable habitat conditions there, which were certainly the most stable among all the waters studied.

Large river

The phenological shift towards the early phase of the wet season was clearly discernible in the larger river (Lukusashi). Just at the beginning of the rainy season in the first half of December, the odonate assemblage was highly distinguished and the most abundant in terms of both species richness and population numbers. Twenty-one species were found and 13 of them (e.g. *Mesocnemis singularis*, *Ceriagrion kordofanicum*, *Pseudagrion glaucescens*, *Gomphidia quarrei*, *Mastigogomphus* cf. *dissimilis*, and *Paragomphus elpidius*) were only recorded in this early phase. This richness was certainly related to diverse microhabitat conditions and easy access to the generally shallow and warm habitat in the low water phase, with the prospect of an approaching high-water phase. The habitat complex included not only stronger main-current parts, but also calmer (partly stagnant) side branches and even a bare seepage puddle on the margin of the riverbed.

In contrast, the complex of riverine habitats in another low-water phase in April. i.e. at the end of the wet season and before a cool phase of the dry season, was very poor:

only five species were recorded and one of them, *Pantala flavescens*, was associated only with side pools remaining after the river flood. Moreover, the odonate abundance was incomparably lower: even the most abundant *Brachythemis lacustris* reached no more than ten percent of the December numbers. This poorness was certainly related to the prospect of the seven-month-long low-water phase beginning from at least three relatively cool months.

A high-water period occurred between these early and late low-water phases, i.e. during the peak of the wet season. Despite appearances, it was quite difficult for dragonflies and damselflies, as the swollen, strongly flowing and deep river was largely unfavourable for reproductive activity. Thus, Odonata were almost totally absent there. On the contrary, they mostly occurred in broadly flooded mouth sections of tributaries, offering calmer and shallower water, and in glades and ravines in the river hinterland. A moderate number of ten species was recorded in the high-water period, but only *Trithemis werneri*, generally known from its relatively late emergence (Tarboton & Tarboton 2019), was recorded solely in this phase of the wet season.

Discussion

Species richness

Clausnitzer et al. (2012) and Dijkstra et al. (2015) assessed the species richness of Odonata in the Afrotropics on the basis of known localities and expert knowledge of habitat requirements and general biogeographic patterns. According to this assessment, the expected species richness in the region of central Zambia that was studied should be fairly high, with 141–160 species per individual river sub-basin (Hydro1k basin). Our 104 species from Chingombe are hardly comparable, as they were collected only in a small area, which was much smaller than any river catchment in this region. What is more, the study area was almost devoid of permanent standing waters, thus its fauna was deficient in species strictly related to these habitats. Considering these facts as well as the species certainly still awaiting discovery in hardly accessible upland localities, the local odonate fauna of the Chingombe environs appeared relatively rich.

The species richness potential of the study area was additionally revealed by discoveries of at least eight species for the first time recorded or unambiguously confirmed in Zambia (Bernard & Daraż 2018; Bernard et al. 2018). These discoveries, along with zoogeographically important records of further 15 species, filled gaps in the previously known distribution ranges and showed that some of them extend further, especially to the south, but also to the west or north (Bernard & Daraż 2018).

Species zonation

An odonate 'river-continuum' sequence (Vannote et al. 1980) was recorded in the study area, from the upper and lower reaches of the mountain stream, down through submontane streams and rivers to the fairly large river draining the rift valley. This spatial sequence was characterised by: a) large-scale interpenetration between the odonate assemblages, with more specific faunas of the mountain stream and large river, and rich, but less specific fauna of submontane watercourses, and b) a fluent replacement of some species with their related

counterparts, for example, more upland species of closed habitats (*Chlorocypha consueta*, *Elattoneura cellularis*) by species related to semi-open and open lower-elevated watercourses (*Platycypha caligata*, *Elattoneura glauca*).

This distinct but not total spatial and ecological segregation resembled a similar situation observed between taxonomically related species along the habitat gradient from small streams to large rivers in the Upper Guinean forest in Liberia and Ghana (Dijkstra & Lempert 2003). Zonation of Odonata along running waters in the Afrotropics, from sources down to a large river, was also studied within a river catchment in SW Ivory Coast (Legrand & Couturier 1985). However, the results of the Zambian and both West African studies are hardly comparable in detail, as they describe different zoogeographical and ecological units with almost totally different sets of odonate species. In Zambia, studies were carried out in miombo and gallery woodland, while in West Africa, this was mostly in lowland rainforest and only partly in the gallery forest of the relatively dry hills of Ghana's Volta Region.

Instead of these substantial differences, several widespread species were recorded in watercourses in both Zambia and the Upper Guinean forest. The position of some these species in the sequence of running waters and the species habitat preferences was still practically the same in these geographically distant regions: a) *Heliaeschna fuliginosa* was significantly related to small mostly shaded streams, heavily loaded with detritus, b) *Orthetrum julia* inhabited streams, mostly small and intermediate, and c) *Mesocnemis singularis* occurred in large rivers with a wide and flat riverbed allowing the persistence of pools and side branches after high water periods (Dijkstra & Lempert 2003 and the results of the present study). In turn, the habitat preferences of some other species seemed to be slightly shifted along the habitat gradient: *Pseudagrion sjoestedti* and *Olpogastra lugubris* were mostly related to large streams and small rivers in central Zambia, while they were more concentrated in large rivers in West Africa. This species shift in the sequence of habitats was most evident in *Pseudagrion sublacteum* and *Trithemis arteriosa*, which were quite common in the open streams and small rivers that we studied in central Zambia, but absent or almost absent from these habitats and occurring only in large rivers in West Africa (Dijkstra & Lempert 2003). However, the latter species preferred similar microhabitat conditions in both regions: calmer or even stagnant, often temporary waters and their parts.

Some other Zambian species recorded by us had their taxonomically related counterparts in similar habitat zones in the Upper Guinean forest (Dijkstra & Lempert 2003). Such pairs were represented by *Notiothemis jonesi* and *Notiothemis robertsi* in small and intermediate shady streams, as well as *Gomphidia quarrei* and *Gomphidia gamblesi* in more open large streams and small rivers.

Phenology

Phenology of Odonata in seasonal Afrotropics is more or less influenced by the wet and dry seasons (e.g. Gambles 1960, Parr 1984, the results of the present study). However, the distinctiveness of the local phenological pattern of the odonate fauna may be related to the rate and specificity of temporary and permanent waters. In the environs of Chingombe, the phenological pattern was generally well-structured due to two distinct peaks – in the first phase of the wet season both in the large river and temporary waters, and at the end of it in the latter.

In the Liwonde National Park in Malawi, situated at a similar latitude and having the same temporal range of the wet season, the phenological pattern of the odonate fauna seemed to be "fuzzier" (see Parr 1984). This was possibly due to the occurrence of permanent standing waters (swamps and lagoons) adjacent to the large river, i.e. the water bodies totally absent in Chingombe. They might have provided favourable conditions for many species throughout the year.

It is worth noting, that many species (e.g. *Pseudagrion acaciae*, *Anax tristis*, *Brachythemis lacustris*, *Nesciothemis farinosa*, *Olpogastra lugubris*, *Tramea basilaris* and *Zygonyx torridus*) were not recorded in Liwonde at the beginning of the wet season in December (Parr 1984), but were well represented in the same phase (month) in Chingombe, and some differences in species occurrence were also recorded in other wet season months. These differences might simply have been a consequence of insufficient Malawian material and/or some local phenological shifts resulting from different local relief and specific features of the water bodies. Difficulties with habitat access and exploration in Liwonde in the wet season (Parr 1984) might have shown the former reason. In turn, the almost total lack of gomphids and scarcity of *Z. torridus* and *O. lugubris* in the Malawian materials compared to our Zambian observations suggested the latter one. It must be stressed that the Malawian Liwonde mostly included a flat valley, while the Zambian Chingombe area also comprised mountains and an upland plateau, thus smaller permanent watercourses might have been markedly different. However, phenology was analysed in Malawi not for the particular types of habitats (as in Chingombe), but only for species, and additionally during the whole year, thus a direct habitat-focused comparison was impossible. Instead of these analytical and interpretative difficulties, the indirect comparison showed that the phenological pattern of local odonate assemblages in the Afrotropics may to some extent differ even within the same biome and at the same latitude due to different and locally specific geomorphological and hydrological conditions.

The phenological rhythm observed in temporary waters of central Zambia was similar to that recorded in the corresponding zone on the opposite site of the equator, in northern Nigeria (Gambles 1960). This mirrored similarity dealt with a) the very early appearance of adults at the beginning of the wet season, b) the emergence generally concentrated at the end of the wet season, but beginning in the rapidly developing species already in the peak of it, and c) presumed very long life of imagines (8–9 months) surviving to the next wet season. Only time ranges of the phenomena were adjusted according to the timing of the wet season in the appropriate hemisphere, e.g. the emergence was concentrated in April in Zambia and in September–October in N Nigeria. In Nigeria, the 'in-advance' activity in places of still non-existing water bodies was, however, even earlier than that recorded in the Chingombe environs: *Lestes virgatus* and *Gynacantha vesiculata* began to oviposit two months before the water body was formed, the former in plant tissues, the latter in mud (Gambles 1960). This was probably an effect of the more prolonged phase of rehydration and forming water bodies during the wet season in northern Nigeria than in central Zambia.

The mass flight of *Pantala flavescens* with some accompanying *Tramea basilaris* just before the first intensive rains also found its mirrored counterpart in Nigeria before the arrival of the northward-moving Intertropical Convergence Zone (Corbet 1999). This pre-rain phenomenon was probably based on true 'veterans' that had survived the long dry season. It might possibly have played the role of the anticipating colonisation of the still dry areas. Mass appearance of "typhoon flies" (presumably *Pantala flavescens*) shortly before the storm was also recorded

in southern China (Tulloch 1929). In contrast, regular annual migration in reversed proportions, mainly *Tramea basilaris* with an admixture of *Pantala flavescens*, occurred in northern Nigeria at the end of the wet season (Gambles 1960). This was typical post-emergence displacement on a large scale. Both these mass displacements seemed to be released by weather conditions: the pre-rain flight by specific conditions announcing approaching storms, i.e. most probably changes in barometric pressure (Tulloch 1929), and the post-emergence migration by intertropical fronts (Gambles 1960).

Acknowledgements

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Tillyard, R., 1924. The dragonflies (Order Odonata) of Fiji, with special reference to a collection made by Mr. H.W. Simmonds, F.E.S., on the Island of Viti Levu. Transactions of the Entomological Society London 1923 III-IV: 305-346.

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