Dragonflies of the Okavango River system

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All dragonfly records from the Okavango River system are compiled from historical publications and the most recent checklists of Botswana and Namibia. A total of 126 species occur in the immediate catchment, excluding the large fossil drainage of the Omatako River. The survey intensity was very different between the river sections, with the Angolan part being almost unexplored. This is reflected in low species numbers from the upper catchment (34), while species numbers in the middle section (91), the Panhandle (74) and the Delta (85) are much higher.

INTRODUCTION

Freshwater ecosystems and in particular river systems, are the most threatened ecosystems worldwide (Abell 2002). Knowledge of the natural biota of freshwater ecosystems and particularly of rivers is crucial for conservation planning (Abell 2002, Wiens 2002). The more common approach in biodiversity assessments is to compile regional or national checklists defined by political boundaries. A useful approach for gathering such information is, however, to work on the river catchment scale (Thieme et al. 2005). Very few studies on Odonata have focussed on the catchment scale, which usually consider smaller catchments, particularly the running water sections (e.g. Bishop 1973, Hawking & New 1999, Worthen 2003).

In this paper we focus on the Odonata of the Okavango River system, which is shared by three countries, Angola, Namibia and Botswana. The Okavango River is the third largest river in southern Africa (Mendelsohn & el Obeid 2004) with its basin covering an area of 192,500 km². The basin straddles sub-humid climatic zones in Angola through semi-arid to arid climatic zones in Namibia and Botswana. In Botswana, the Okavango River drains into the Okavango Delta – a world-class wetland. The Okavango Basin and particularly its Delta is also one of Africa's last remaining pristine aquatic ecosystems in ecological terms. Chemical pollution of the water and damming is rare (the latter occurring in the upper section), whereas no channelling occurs. The natural vegetation is also widely intact, except for some parts in the upper Okavango system and on the Namibian side of the middle section of the Okavango (*vide* Mendelsohn & El Obeid 2004).

The biological communities of the river system are only partly documented. For example, fish diversity has only been surveyed in the middle section of the Okavango and in the Delta (Hay *et al.* 1996, Merron & Bruton 1993). There are no studies thus provide an overview about the odonate fauna of the whole river system. The best-known section is surely the Okavango Delta, which has seen about 30 expeditions or at least visits by odonatologists contributing to the species list. The knowledge about the Okavango Delta has first been compiled by Pinhey (1976) and 30 years later updated by Kipping (2003a, b, 2006), both providing country checklists of Botswana. By contrast, the river upstream the Delta and the Panhandle has long been neglected. There are few historical records from the Namibian and Angola parts of the catchment. Curtis (1991), Martens *et al.* (2003) and Suhling *et al.* (2006) compiled the records available for the Namibian part of the Okavango, again as part of country checklists. Most of records of the Angolan part of the river system have been collected during only two expeditions by A. Monard in 1928/29 and 1932/33 and have been

published by Ris (1931) and Longfield (1947). Pinhey (1966, 1975) added a few records from the Angolan part of the Okavango Basin.

The aim of this paper was to compile the knowledge about the Odonata fauna of the Okavango River system in a single review, which is otherwise spread over various sources (*vide supra*). We provide a broad overview about the dragonfly fauna of the different sections of this river system and identify the most urgent research gaps.

MATERIAL AND METHODS

STUDY AREA

The Okavango River flows southwestwards across the Kalahari basin from the high elevation of Planalto do Bié between 1,700 and 1,800 m on the Basin's rim to Okavango Delta (940 m), where the river ends in the centre of the Kalahari (Figure 1). The Okavango Basin covers an area of 192,500 km². The catchment can be subdivided into four major sections (Mendelsohn & El Obeid 2004).

- The active upper catchment, being the largest area of the catchment (111,000 km²), consists of the headwaters and upper river sections of the Okavango River (here called Cubango/Kavango) and of the Cuito River, which is the major tributary to the Okavango. This section receives the highest rainfall and therefore several tributaries originate in the southern rim of the Planalto do Bié in Angola, where the rivers are characterised by steep gradients causing erosion and forming incised valleys and sometimes valley marshlands.
- The middle section consists of the inactive parts of the Cubango/Kavango and of the Cuito, where only few and usually ephemeral tributaries join the main course of the river. Here the river forms broad floodplain valleys but still has swiftly flowing sections and even some rapids, e.g. at Popa Falls and Andara.
- The Panhandle begins a few kilometres north of the Botswanan-Namibian border in the Mahango Game Reserve, from where it extends south to the Gumare fault. Most of the water flows in meandering channels, surrounded by broad marshes with Papyrus and reeds and dense riverine woodland. Like the Delta the Panhandle is a deposition area. The Panhandle usually is recognised as part of the Delta, but we treat it separately due to its different structure.
- The Delta is an alluvial fan in the arid Kalahari of about 40,000 km². It is characterised by numerous channels and permanent as well as seasonal swamps, which may expand or contract depending on the rainfall in the upper catchment and on local rainfall in the Delta.

In years with good rains in Angola the water may flow as far south as the Makgadikgadi Pans, which is often considered as part of the catchment as well It may be connect with the Zambezi River system via the Selinda Spillway and the Kwando/Chobe River, or may reactivate channels to Lake Ngami. Although fossil drainage lines are part of the catchment, the largest being the Omatako River originating in central Namibia, we did not consider the fauna of these non-permanent systems for this review. Only information on the dragonfly fauna Of the Omatako is available (Suhling et al. 2006). We therefore follow Mendelsohn & El Obeid (2004) in excluding the fossil drainages and the Makgadikgadi Pans from the immediate Okavango catchment for this study.

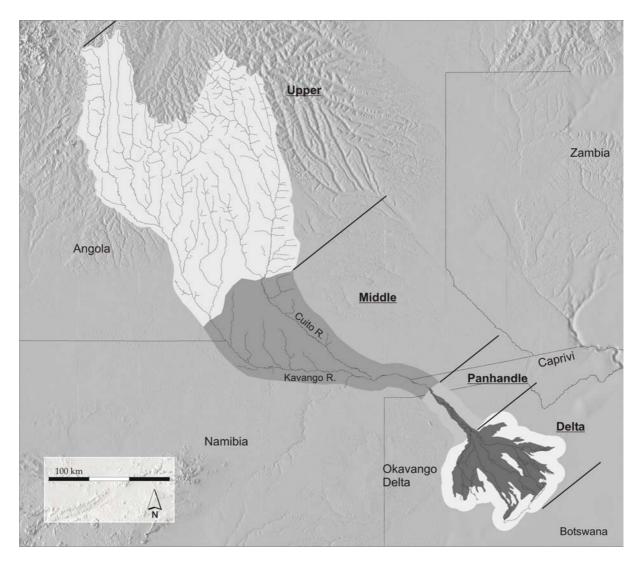


Figure 1. Overview of the Okavango River system, depicting the four river sections.

DATA SOURCES

For an overview of the dragonfly diversity of the Okavango catchment as defined above, we compiled published species distribution data from all sections of the river system. The data sources for the upper catchment are limited to few publications of Ris (1931), Longfield (1947), and Pinhey (1966, 1975) and no recent data are available at all. Records from the Chimporo River in Angola were assigned to the Okavango system, although it may actually be part of the Cuvelai system. For Namibia and Botswana we extracted species distribution data on the Okavango system from the databases of the respective country checklists (Kipping 2006, Suhling *et al.* 2006). The data of those checklists include all published records as well as hitherto unpublished records by the authors. All records were georeferenced and assigned to the respective river sections as described above.

RESULTS

The survey intensity was different between the respective river sections (Figure 2). Only a few localities, with a low number records, were sampled in Angola. These figures increase downstream. By far best surveyed area was the Delta, where 125 localities have been sampled and more than 2100 species locality records have been made.

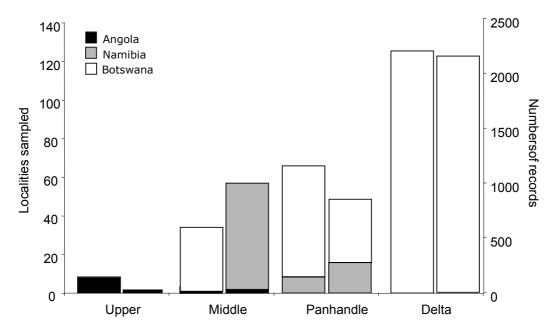


Figure 2. Numbers of localities sampled (left bars) and numbers of records (right bars) in the different river sections and the three countries involved.

A total of 126 species have been recorded from the Okavango River catchment to date (Table 1). In the badly explored upper section only 34 species were recorded, of which, however, a relatively high amount of 9 species have never been recorded in the lower sections. The highest number of species (91) was found in the middle section, whereas the figures were slightly lower in the Panhandle (74) and in the Delta (85).

DISCUSSION

The dragonfly fauna of the Okavango River comprises more than half the number of species recorded in Angola, Botswana and Namibia together (202 species). Given that the upper catchment consists of more than half of the Okavango Basin area it is obvious that the dragonfly diversity in that section is clearly underestimated. The 34 species are from 35 records, which is about one species per record. In comparison, in the middle section 91 species derive from 993 records and 84 species from 2134 records in the Delta. Although this comparison does not allow an estimate of the likely odonate species diversity of the upper Okavango catchment it suggests a much higher species number, which could be as high as in the middle section, or even higher with new species to science being quite likely.

If the diversity of running water systems in the upper section is also taken into account, then higher or at least comparable diversity to the more uniform middle section can be assumed. The upper section of the Okavango River should therefore be a research priority for the future.

Although the data recorded for the upper section is still poor, it is obvious that a number of specific species can be expected. Some species that demand considerable shade, i.e. depend on dense, pristine riverine forest, occur along the river, for instance *Chlorocypha crocea*. The shade factor seems generally to be a major determinant in the community composition of tropical African rivers as shown for western Africa (Dijkstra & Lempert 2003). Deforestation therefore affects communities significantly (Clausnitzer 2003). We expect that more such shade loving species will occur in the upper section of the Okavango River. For instance, the genus *Umma* should be represented in these reaches, e.g. by *U. femina* that occurs in the neighbouring upper Kunene catchment.

The middle section of the river is characterised by a high number (13) of gomphid species. They are typical running water species, whose larvae live in the sediment of the rivers. The larval forms with breathing snorkels are apparent, some of them living deeply burrowed into soft sediment, e.g. *Neurogomphus* and *Phyllogomphus*. *Crenigomphus kavangoensis* is so far endemic to this river section (see Suhling *et al.* 2006). Major parts of this section are ecologically more uniform and so is the dragonfly fauna. This section is also most affected by deforestation of the riverine forest, which on the Namibian banks is widely eliminated except for few remnants (Thieme *et al.* 2005). Stretches that still have forest remnants usually host more than 40 species. Even higher species numbers occur along the few rapids at Andara and Popa Falls, which also carry the largest forest remnants. Typical species at the rapids are for instance Platycycpha caligata, Paragomphus cataractae, Zygonyx natalensis and Z. torridus, all which have larvae with characters that allow them to live in the current, e.g. tigmotaxis in Zygonyx. The reproduction behaviours of P. caligata and Z. natalensis are also related to the fast currents (Martens & Rehfeldt 1989, Martens 1991). At Popa and Andara these species are accompanied by shade loving species such as *Phaon iridipennis* and *Trithemis aconita*.

The Panhandle is a section where the riverine fauna is gradually replaced by the swamp fauna of the Delta. A typical ecological feature is the presence of shady riverine forest along the channels and extended *Papyrus* swamps, which enables the occurrence of e.g. *Chalcostephia flavifrons*, *Trithemis aconita* or *Rhyothemis fenestrina* in fairly large numbers. In some areas at the Panhandle margin human population growth and landuse lead to degradation and ecological change through cutting of those forests. Only one species, *Lestinogomphus silkeae*, occurs in the Panhadle that has not yet been encountered elsewhere in the river system.

Finally, the Delta represents an environment that is gradually changing from perennial to ephemeral swamps. This is as well reflected in the dragonfly fauna. Gomphid species become scarce but Zygoptera and libellulids reach high diversity. The spatial linkage and immediate neighbourhood of permanent channels, ephemeral secondary floodplains, short duration rainpools and marginal forests on the islands, result in the coexistence of riverine species, widespread savannah species and species of large perennial swamps. We would like to stress that from an ecological point of view, as in other parts of the river system, the separation of Panhandle and Delta used in this paper and often generally in literature is rather arbitrary. Habitat conditions as in the Panhandle are also to be found in the permanent flooded northern part of the Delta, changing gradually into more ephemeral conditions along the gradient of decreasing flood duration periods. Remarkable long and short term fluctuations in floodwater inflow, as well as the spatial changes of flood events, cause the Delta to be the more dynamic part of the river system (*vide* McCarthy et al. 2000). The permanent presence of water throughout the year transforms the Delta into a diversity hotspot in the arid interior of southern Africa.

Several species occurring in the Delta and Panhandle (up to Popa Falls), show a disjunct distribution pattern between the Delta and Lake Bangweulu swamps, such as *Trithemis brydeni* and *Anax bangweulensis*. We expect them to occur in swamps between these two areas as well, such as the Barotse Floodplains or the Kafue Flats in Zambia (cf. Kipping 2006).

The taxonomic status of some of the recorded species is not clear, whereas the occurrence of others need to be confirmed. The status of Onychogomphus rossii described by Pinhey (1966) from one specimen needs clarvification, as is actually the case for many species of the genus in Sub-saharan Africa (Dijkstra 2003). The records of Zygonoides occidentis and Crenigomphus hartmanni (both Longfield 1947) are likely erroneous. The former is a good species occurring predominantly in the Congo basin, except for the one record in the middle section of the Okavango, whereas the sister species Z. fuelleborni is common from the Kunene to the Zambezi catchments (Dijkstra et al. 2006). C. hartmanni may occur, but the record of a female may belong to C. kavangoensis, which is common at the river but was unknown at the time of the record. The females of the species of Crenigomphus s.str. are not easy to distinguish. The presence of T. stictica in the upper catchment also needs proof. In the middle section as well as in the Delta a new species of Trithemis has recently been identified that is very similar to T. stictica. We were not able to examine the material from Angola, but may be possible that the new species also occurs there. Finally, the record of Nesciothemis minor in the Delta by Pinhey (1976) remains doubtful (Kipping 2006b). It has never been re-recorded and otherwise only occurs in western Africa. On the other hand, this also applies to B. wilsoni, which has been recovered recently in the Delta (Kipping 2006b).

The Okavango River has a high level of dragonfly diversity, which is surely still underestimated due to the poor record from Angola. This preliminary compilation of the dragonfly fauna may therefore serve as a baseline for future studies.

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Table 1 List of s	necies recorde	d in the d	lifferent sections	of the C	Okavango River system.
TADIC I. LISU OF S	pecies recorde	a m une a	merene secuons	or the C	mavango mver system.

Species	Upper section	Middle section	Panhandle	Delta
CALOPTERYGIDAE	11			
Phaon iridipennis (Burmeister, 1839)	-	х	х	-
Chlorocyphidae	-	-	-	-
Chlorocypha crocea Longfield, 1947	х	-	-	-
Platycypha caligata (Selys, 1853)	х	х	-	-
Lestidae				
Lestes dissimulans Fraser, 1955	-	-	х	х
L <i>estes pallidus</i> Rambur, 1842	-	х	х	х
Lestes pinheyi Fraser, 1955	-	х	х	x
Lestes plagiatus (Burmeister, 1839)	-	-	-	x
Lestes tridens McLachlan, 1895	-	-	-	x
Lestes virgatus (Burmeister, 1893)	-	-	-	x
COENAGRIONOIDEA				
Aciagrion steeleae Kimmins, 1955	-	-	-	x
Africallagma subtile (Ris, 1921)	-	х	х	-
Agriocnemis angolensis Longfield, 1947	-	х	х	-
Agriocnemis exilis Selys, 1872	-	х	х	x
Agriocnemis gratiosa Gerstäcker, 1891	-	х	х	x
Agriocnemis ruberrima albifrons Balinsky, 1963	-	-	х	x
Agriocnemis victoria Fraser, 1928	-	-	-	x
Azuragrion nigridorsum (Selys, 1876)	-	-	-	x
Ceriagrion glabrum (Burmeister, 1839)	х	х	х	x
Ceriagrion katamborae Pinhey, 1961	-	-	х	x
Ceriagrion suave Ris, 1921	-	х	х	х
Elattoneura glauca (Selys, 1860)	х	X	X	x
Ischnura senegalensis (Rambur, 1842)	-	X	X	x
Mesocnemis singularis Karsch, 1891	х	x	X	_
Pinheyagrion angolicum (Pinhey, 1966)	-	x	-	х
Pseudagrion acaciae Förster, 1906	-	X	х	x
Pseudagrion assegaii Pinhey, 1950	-	X	х	х
Pseudagrion coeleste Longfield, 1947	-	x	X	x
Pseudagrion commoniae nigerrimum Förster, 1902	-	X	X	X
Pseudagrion deningi Pinhey, 1961	-	X	X	x
Pseudagrion fisheri Pinhey, 1961	-	-	-	x
Pseudagrion glaucescens Selys, 1876	-	X	X	X
Pseudagrion hageni tropicanum Karsch, 1893	x	-	-	-
Pseudagrion hagoni Fraser, 1955	-	x	x	x
Pseudagrion helenae Balinsky, 1964	-	-	-	X
Pseudagrion inconspicuum Ris, 1931	x	-	-	-
Pseudagrion massaicum Sjöstedt, 1909	x	x	-	x
Pseudagrion massarum Sjöstell, 1909	-	-	_	X
Pseudagrion rufostigma Longfield, 1947	-	-	_	X
Pseudagrion rajostigma Longfield, 1947	x	-	-	-
Pseudagrion sinsonryense Kis, 1921 Pseudagrion sjoestedti jacksoni Pinhey, 1961	x _	- v	- x	
Pseudagrion spornatum Selys, 1881		x -	X _	x -
	x			
Pseudagrion sublacteum (Karsch, 1893)	-	X	X	X
Pseudagrion sudanicum rubroviride Pinhey,1955	-	х	х	x
GOMPHIDAE		-		
Crenigomphus cornutus Pinhey, 1956	-	Х	-	-
Crenigomphus hartmanni (Förster, 1898)	х	-	-	-
Crenigomphus kavangoensis Suhling & Marais, 2006	-	X	-	-
Gomphidia quarrei (Schouteden, 1934)	-	X	-	X

Ictinogomphus ferox (Rambur, 1842) Lestinogomphus angustus Martin, 1911	_	X X	X X	X _
Lestinogomphus silkeae Kipping, 2006	_	-	x	_
Mastigogomphus sp.	-	x	-	-
Nusugggomphus sp. Neurogomphus cocytius Cammaerts, 2004	_	X		_
Onychogomphus rossii Pinhey, 1966	x	-	-	-
Paragomphus rataractae Pinhey, 1966			-	-
Paragomphus cataractae Filiney, 1965 Paragomphus cognatus (Rambur, 1842)	-	X X	-	-
	-		-	
Paragomphus elpidius (Ris, 1921)	-	X	-	X
Paragomphus genei (Selys, 1841)		X	х	Х
Paragomphus sabicus Pinhey, 1950	-	X	-	-
<i>Phyllogomphus selysi</i> Schouteden, 1933 AESHNIDAE	-	Х	-	Х
Anax bangweuluensis Kimmins, 1955	-	-	х	х
Anax ephippiger (Burmeister, 1839)	-	х	х	х
Anax imperator Leach, 1815	-	х	х	x
Anax tristis Hagen, 1867	-	х	-	x
MACROMIIDAE				
Phyllomacromia contumax Selys, 1879	-	х	х	х
Phyllomacromia kimminsi Fraser, 1954	-	-	-	x
Phyllomacromia overlaeti (Schouteden, 1934)	-	х	х	-
Phyllomacromia picta (Selys, 1871)	-	х	х	х
LIBELLULIDAE				
Acisoma panorpoides ascalaphoides Rambur,1842	-	х	х	х
Acisoma trifidum Kirby, 1889	-	х	-	_
Aethiothemis discrepans Lieftinck, 1969	-	x	х	-
Aethriamanta rezia Kirby, 1889	_	X	x	х
Brachythemis lacustris (Kirby, 1889)	х	x	x	
Brachythemis leucosticta (Burmeister, 1839)	X	X	x	х
Brachythemis wilsoni Pinhey, 1952	-	-	-	x
Bradinopyga cornuta Ris, 1911	_	х	-	-
Chalcostephia flavifrons Kirby, 1889	_	-	х	х
Crocothemis erythraea (Brullé, 1832)	х	х	x	x
Crocothemis sanguinolenta (Burmeister, 1839)	X	-	-	x
Diplacodes deminuta Lieftinck, 1969	-	х	х	x
Diplacodes lefebvrii (Rambur, 1842)	х	x	x	x
Diplacodes luminans (Karsch, 1893)	-	X	x	x
Hemistigma albipunctum (Rambur, 1842)	_	x	x	x
Nesciothemis farinosa (Förster, 1898)	х	X	x	x
Nesciothemis minor Gambles, 1966	-	-	-	x
Olpogastra lugubris Karsch, 1895	-	х	х	X
Orthetrum abbotti Calvert, 1892	x	-	-	-
Orthetrum brachiale (Palisot de Beauvois, 1817)	А	x	x	x
Orthetrum caffrum (Burmeister, 1839)	х	X	x	-
Orthetrum chrysostigma (Burmeister, 1839)	X	X	X	x
Orthetrum guineense Ris, 1910	X	X	-	-
Orthetrum icteromelas cinctifrons Pinhey, 1970	-	X	x	x
Orthetrum machadoi Longfield, 1955	-	X	X	X
Orthetrum mathaan Hongheid, 1955 Orthetrum robustum Balinsky, 1965	_	-	x	X
Orthetrum robustum Dainisky, 1965 Orthetrum trinacria (Selys, 1841)	_	x	x	X
Palpopleura deceptor (Calvert, 1899)	-	-	x	-
Palpopleura lucia (Drury, 1773)	x	x	- -	x
Pantala flavescens (Fabricius, 1798)	X	X	x	X
Parazyxomma flavicans (Martin, 1908)	- -	X	x	X
i ana promina juanano (martin, 1900)	-			
Rhyothemis fenestrina (Rambur, 1842)	_	X	X	X

Rhyothemis semihyalina (Desjardins, 1832)	-	х	x	х
Sympetrum fonscolombii (Selys, 1840)	-	х	x	х
Sympetrum navasi Lacroix, 1921	-	x	X	х
Tholymis tillarga (Fabricius, 1798)	-	x	X	х
Tramea basilaris (Palisot de Beauvois, 1807)	х	x	X	х
Tramea limbata (Desjardins, 1832)	-	-	-	-
Trihemis aconita Lieftinck, 1969	-	x	X	-
Trithemis aequalis Lieftinck, 1969	-	х	-	х
Trithemis annulata (Palisot de Beauvois, 1807)	-	х	x	х
Trithemis arteriosa (Burmeister, 1839)	х	х	x	х
Trithemis brydeni Pinhey, 1970	-	-	-	х
Trithemis donaldsoni (Calvert, 1899)	-	х	-	-
Trithemis dorsalis (Rambur, 1842)	х	-	-	-
Trithemis furva Karsch, 1899	х	x	-	-
Trithemis hecate Ris, 1912	-	x	X	х
Trithemis kirby ardens (Gerstäcker, 1891)	х	х	-	х
Trithemis monardi Ris, 1931	-	x	X	х
Trithemis pluvialis Förster, 1906	х	-	-	-
Trithemis sp. nov. (undescribed)	-	х	х	х
Trithemis stictica (Burmeister, 1839)	х	x	-	-
Urothemis assignata (Selys, 1872)	-	-	x	х
Urothemis edwardsii (Selys, 1849)	х	х	X	х
Zygonoides fuelleborni (Grünberg, 1902)	-	х	x	-
Zygonyx natalensis (Martin, 1900)	х	х	x	-
Zygonyx torridus (Kirby, 1889)	-	х	-	-