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CHAPTER 8

FRESHWATER MOLLUSCS OF THE ZAMBEZI RIVER BASIN

Cornell Dudley

8.1 INTRODUCTION

The Zambezi River, its tributaries and wetlands make up one of Southern Africa's most important natural resources. Given the rapid rate of development and population growth in this region there is intensifying pressure on these resources. As a consequence, the river's wetlands and their associated biodiversity are under increasing threat. In order to more formally evaluate these resources, IUCN-ROSA, in conjunction with the Canadian International Development Agency, initiated the Zambezi Basin Wetlands Conservation and Resource Utilisation Project in 1996. This project is aimed at ensuring the wise use of the natural resources of the wetlands of the Zambezi Basin, focussing in particular on four project sites – the Barotse floodplains, the floodplains and swamps of the Chobe/Caprivi region, the wetlands of the Lower Shire Valley and the Zambezi Delta. One of the project activities is to evaluate the importance of biodiversity from a conservation perspective, both for the four wetland areas and for the wetlands of the basin as a whole. As part of this project technical reviews on the distribution, biogeography, ecology, importance, conservation interest and status of selected biological groups are required, of which this review of the basin's freshwater molluscs forms part.

The freshwater molluscs are examined from both biodiversity and biogeographical perspectives. A analysis of the fauna is presented and checklists of the basin are included. In particular, the basin's centre of biodiversity, Lake Malawi, is compared with Lake Tanganyika, and the molluscs of the river basin are discussed in relation to the other major river basins of the continent – the Congo, the Nile and the Niger. Conservation aspects are evaluated and suggestions for future investigations are presented. Also included is a discussion of the distribution and importance of the genera *Biomphalaria* and *Bulinus*, intermediate hosts of *Schistosoma* species, which are important blood flukes of man.

In most cases it is not difficult to define ecological limits for freshwater molluscs. Problems arise when coastal streams, estuaries and lagoons are considered, as a few species occupy both brackish and freshwater habitats, e.g. streams flowing into mangrove swamps, or near tidal influences. A few such species have been included in this review.

Almost all mollusc families living in freshwater are, from a geological point of view, old families, possibly dating from before the Mesozoic era. Consequently they are of world wide distribution (Danish Bilharziasis Laboratory 1998). Gastropod (snails) classification is in a continuing state of revision and it will be some time before a system comes to be generally agreed for the groups of higher rank (Brown 1994). The freshwater bivalves (mussels, clams) have been a neglected group as they are of little economic or medical importance. Their systematics are even more difficult as species show great variation in morphology with relatively few constant characters. It is easy to recognise families but generic recognition often entails anatomical examination. Without sufficient experience of the family and country of origin, defining a species is often very difficult, and occasionally impossible (Danish Bilharziasis Laboratory 1998, Mandahl-Barth 1988).

The Gastropoda, or snails, are commonly divided into two major subclasses, the Streptoneura (including the Prosobranchia) and the Euthyneura (including the Pulmonata). Prosobranchs have a comb-like gill (branchia/ctenidia) situated in the mantle cavity in front of the heart and are entirely aquatic. Attached to the foot is a horny or calcareous operculum which can be used to close the shell aperture. Sexes are separate. The group is most varied in the larger lakes and rivers of the continent and may contribute a major part of the invertebrate benthos biomass (Leveque 1972 in Brown 1994, Machena & Kautsky 1988). Species may be found to depths of 150-200 m.

Pulmonates include terrestrial as well as aquatic species and have a mantle cavity serving as a lung. No gills are present although planorbid species have a gill-like respiratory organ in the mantle cavity called the pseudobranch. An operculum is lacking. Individuals are hermaphroditic. Pulmonates are most abundant in shallower (< 10 m) smaller water bodies, including seasonal rain pools.

The second class, Bivalvia (mussels and clams), has, as the name implies, a pair of hinged shells (valves) which contain a pair of gills (ctenidia) on each side of the visceral mass and a rudimentary foot, all within the mantle cavity. The larvae of the group Unionacea are parasitic on the gills of freshwater fish, while those of the group Sphaeriacea are incubated in brood chambers in the inner gills. Eventually, the young bivalves drop off and bury themselves in the mud, only their posterior end reaching up into the water. All are filter feeders.

8.2 LITERATURE REVIEW

The earliest records of freshwater molluscs in the Zambezi Basin were the result of collections made by early travellers and explorers in the middle of the 19th century. Of note were the collections of W. Peters in Mozambique and the Zambezi Valley in 1843-48 (von Martens 1859, 1879) and that of J. Kirk of the David Livingstone expedition in 1859, who collected along the Upper Shire River and, more significantly, in Lake Nyasa (Lake Malawi) (Dohrn 1865). The collections by J. Speke of the unusual thalassoid (marine-like) gastropods in Lake Tanganyika in 1858 (Woodward 1859) stimulated the first truly scientific expeditions to study freshwater organisms, including molluscs, in tropical Africa. While the focus of these expeditions was outside the Zambezi area, each of the first three (1895, 1899, 1904) visited and collected in the environs of Lake Malawi (Cunnington 1920).

The discovery that the snails *Bulinus truncatus* and *Biomphalaria alexandrina* of Egypt were the intermediate hosts of the serious human parasitic disease, bilharzia (Leiper 1915, 1918), initiated the modern phase of malacology in tropical Africa. Three important regional monographs on the non-marine molluscs followed: Mozambique (Connolly 1925, 1939), Belgian Congo (now the Democratic Republic of the Congo) (Pilsbry & Bequaert 1927) and South Africa (Connolly 1939). Although two of the three are focussed on regions outside the Zambezi Basin, all remain indispensable today as they apply to a much wider fauna and geographical area. Additionally, Haas (1936) collected widely in the basin and was one of first to add biogeographical data and considerations as regard stream basins and similar features.

In the last thirty years there has been a considerable improvement in our knowledge of freshwater mollusc biology, taxonomy and distribution within the basin. Haas (1936, 1969) and Mandahl-Barth (1988) reviewed the taxonomic disarray of the bivalves, particularly the Unionidae, consolidating the disparate fauna to a more realistic number of species. The freshwater snails of Angola were reviewed by Wright (1963), while Mandahl-Barth (1968a) published on the fauna of the upper

reaches of the SE Congo Basin. In 1961, Azevedo *et al.* provided a comprehensive account of the snails and bivalves of Mozambique as did Crowley, Pain & Woodward (1964) and Mandahl-Barth (1972) for Lake Malawi. Much later, Brown *et al.* (1992) gave an account of the freshwater snails of East Caprivi and the lower Okavango River in Namibia and Botswana. Recently, in 1996, Appleton wrote an illustrated guide to all freshwater molluscs (gastropods and bivalves) of Southern Africa.

The most significant work on freshwater gastropods to date is that by Brown (1980, 1994), which reviews in great detail our knowledge on the taxonomy, biogeography, ecology, biology and medical importance of the freshwater snails of Africa. A major catalogue on the freshwater bivalves of Africa (Daget 1998) has recently been published. This text provides complete synonymies and references for every species and includes an extensive bibliography. In this review I have followed the systematics of these two works.

A large part of the work on the freshwater molluscs (particularly snails) since World War II, has been supported by the World Health Organisation and national governments in their quest to understand the complex relationships between the numerous parasites of humans and livestock (schistosomes, amphistomes and liver flukes) and their intermediate snail hosts. Substantial support remains for malacological research in the field and laboratory today and important institutional work continues to be done by the Blair Research Institute in Harare, Zimbabwe, the Biomedical Parasitology Section of the Natural History Museum in London and the Danish Bilharziasis Laboratory in Charlottenlund (Brown 1994). The latter institute has produced numerous field guides for gastropods which cover all of Africa (Danish Bilharziasis Laboratory 1977, 1982, 1987, 1989, 1993, 1998). These guides are profusely illustrated with careful line drawings and practical keys.

8.3 THE ZAMBEZI RIVER BASIN

The Zambezi River, originating on Kalene Hill in northwestern Zambia, flows nearly 2600 km before entering the Mozambique Channel. It is Africa's fourth largest river system draining approximately 1.57 million km² (Allanson *et al.* 1990) which includes substantial areas of Angola, Malawi, Mozambique, Zambia, and Zimbabwe, and much smaller portions of Botswana, Namibia and Tanzania. The river is often divided into three distinct biogeographic sections – the Upper, Middle and Lower Zambezi (Bell-Cross 1965b, Timberlake 1998).

The Upper Zambezi, from its source in Zambia, passes through Angola and Barotseland (Zambia) to Victoria Falls, a distance of approximately 1100 km. Also included are the Kwando River, Chobe/Caprivi and Linyanti system, the Okavango River, Okavango Swamp, Botletle River and Makadikgadi Pans system and the Kafue system. Although not always hydrologically linked, during periods of high rainfall the first two systems flow into each other and hence are unified biologically (Beadle 1981, Davies 1986, Schlettwein *et al.* 1991). The Kafue River joins the Zambezi below the Victoria Falls. The Upper Zambezi typically comprises a series of broad floodplains, such as those of Barotseland, which are separated by low sand plateaux set in a comparatively old landscape. Dense *Brachystegia* woodlands and extensive grasslands are common; swamps are scattered and generally small.

The Middle Zambezi, including its principal tributary the Luangwa, encompasses a section of similar length between Victoria Falls and the Lupata Gorge downstream from Tete. It is dominated by two large dams, Lake Kariba and Lake Cabora Bassa. Originally a 'sand bank' river (Symoens

et al. 1981), the present character of the Middle Zambezi, since the construction of the two huge dams, is of a regulated river running through a combination of narrow gorges and broad valleys in a hot dry landscape of deciduous woodland. Floodplains are very limited. With the increased lacustrine and slow water environments in what was a fast moving river, the Upper and Middle Zambezi are becoming more ecologically homogeneous (Davies 1986, Timberlake 1998).

From the Lupata Gorge, the Lower Zambezi is broad, often comprising many anastomosing channels with shifting sandbanks, until it reaches the sea at Chinde, nearly 400 km downstream (Timberlake 1998). The Shire River, which begins as an outflow from Lake Malawi and drains much of southern Malawi, passes through the Elephant and Ndindi Marshes and then joins the Zambezi River below Mutarara in Mozambique. The Zambezi Delta starts some 120 km from the coast and consists of extensive areas of grassland and wetland with few trees. Towards the coast, expansive areas of mangroves flank mud-lined tidal creeks. The coastal extent of the delta stretches 290 km from Quelimane in the north to Beira in the south (Davies 1986).

Lake Malawi lies within a narrow steep-sided rift valley biogeographically separated from the Zambezi River by a series of turbulent cataracts dropping 280 m in a distance of 80 km along the Middle Shire River.

The modern course of the Zambezi River is relatively young (1-2 million years BP) and its earlier history has been rather unstable (King 1978, Thomas & Shaw 1988). The ancient proto-Upper Zambezi, including the proto-Chambeshi, the headwaters of the Kasai, the proto-Kafue and the Kwando and Okavango rivers, drained a sizeable portion of the Central African Plateau and flowed out through eastern Botswana and northern South Africa via the Limpopo River to the sea. However, Tertiary movements altered many of the older divides between the Congo, Zambezi and Limpopo systems. The headwaters of the Upper Zambezi (proto-Chambeshi and headwaters of the Kasai, 200 km north of the present divide) were back-tilted and now flow in a reverse direction through the swamps to the Congo drainage. In the early Pliocene, violent tectonic activity caused an interruption of the flow of the proto-Kafue, Kwando and Okavango rivers causing the formation of the several palaeo-lakes in the Caprivi area. These events led to the capture of the proto-Upper Zambezi by the Middle Zambezi in the late Pleistocene. The evolution of the Middle and Lower Zambezi is less clear but there is some evidence that the river's exit at Chinde is, at least in evolutionary terms, relatively recent (Tinley 1977). Lake Malawi may have originated in the Miocene, at least its deep northern basin, but its present form is 1-2 million years old (Bowmaker *et al.* 1978, Fryer & Iles 1972).

At present, many watersheds are low between African river basins and during flood season there may be a nearly continuous sheet of water between them (Beadle 1981). For example, the Kamawafura River, a Congo tributary, and the Kanjita stream, a tributary of the Zambezi, have adequate water in channels and pools with continuous links for fish exchange. Their fish faunas indicate some exchange between the two systems via river capture and high flood levels in past pluvial periods (Beadle 1981, Bowmaker *et al.* 1978). Even the upper tributaries of the Cuanza and Cunene Rivers of Angola share watersheds with the Cubango and Kwando rivers, which drain into the Okavango Basin and Zambezi River, respectively (Beadle 1981). Such fish exchanges among river systems have considerable implications for the dispersal of some unionids which have parasitic larval stages (glochidia/lasidium) living on the gills of fish before dropping to the substrate to complete their development (Appleton 1979).

In conclusion, during the Pleistocene, extensive parts of the Central African Plateau were connected hydrologically and wetland organisms had an easy means of dispersal across them. At the same time the palaeo-wetlands fluctuated greatly in extent, primarily in response to large changes in climate.

8.4 THE MOLLUSCAN FAUNA

There are 102 freshwater and brackish water molluscs present, or very likely present, in the Zambezi Basin (including Lake Malawi). Classification of these species and sources for the records are given in Table 8.1, while Table 8.2 shows their distribution across the Zambezi Basin and their habitat.

8.4.1 Biodiversity and distribution of groups

Restricting the analysis to only the 90 indigenous strictly freshwater molluscs (Table 8.3), Gastropoda make up the majority of species (63 species, or 70%). This proportion is slightly smaller than that found in continental tropical Africa as a whole (76%; from Brown 1994, Daget 1998, Mandahl-Barth 1988). Gastropods are able to survive and reproduce in a wide range of freshwater environments including small temporary rain pools, floodplains, swamps, small and large rivers with diverse substrates and shallow to deep lakes. The larger bivalves tend to be restricted to the benthos (bottoms) of stable aquatic habitats like larger rivers and lakes or dams, although smaller species occur in many water bodies including small streams, pans and dams (Appleton 1996, Curtis 1991).

Endemism is high in both subclasses of gastropods, but this is due almost entirely to the contribution of Lake Malawi species (listed in Table 8.4). Out of the 23 endemics, 19 (78%) are found only in the lake. In fact, over half (52%) of all the strictly freshwater mollusc species found in the Zambezi Basin have been recorded from Lake Malawi. Endemism of bivalves is more directly associated with deep lakes and there is only one endemic (*Mutela zambesiensis*) not found in the lake.

Lake Malawi attracted the earliest collectors of molluscs in the region and by the turn of the century, 41 of the 47 species now recorded (87%) were already described. No more than a third of the Zambezi Basin species have been described this century, 15 since 1950. This is a significantly different situation to that of the terrestrial gastropods of Malawi in which approximately 50% were described in this century and nearly 12% in the last 18 years (van Bruggen 1994). Nevertheless, owing to changes in nomenclature the number of species currently accepted in the region is considerably fewer than that thought to be present early in this century. Many of the earliest species descriptions were based on superficial characters of shell size and structure with little reference to important anatomical differences (Brown 1994, Crowley *et al.* 1964, Mandahl-Barth 1988). This has been particularly true of the bivalves of the Great Lakes where in Lake Tanganyika 75 species of Unionidae were reduced to 5 species, and in Lake Malawi 15 species were reduced to 3 (Mandahl-Barth 1988). For gastropods, Crowley *et al.* (1964) cite Bourguignat as an example, listing at least 24 synonyms of *Melanoides polymorpha* that were described by him in 1889.

Among the gastropods, the Streptoneura (prosobranchs) of the basin are proportionally under-represented when compared to the Afrotropical Region, and the Euthyneura (pulmonates) are over-represented (Table 8.3). Using the number of species by subclass and family from Brown (1994, Table 2.1), but restricting the numbers to only those families that are found in the Zambezi Basin and excluding introduced species, species of coastal brackish water and species of Palaearctic affinity, we see that the prosobranchs represent about 75% of the gastropods in the Afrotropical Region, while in the basin prosobranchs only represent 52%. However, the prosobranchs include 18 out of the 23 endemic gastropods, again 16 coming from Lake Malawi. This difference between the subclasses is more striking when we note that the Zambezi Basin contains 40% of the species

of pulmonates known from the Afrotropical Region relative to the prosobranchs' 15%. The proportions of prosobranchs in Lake Malawi show only slightly more "normal" values (57% vs 43%)(see Table 8.5).

The only introduced species to the basin are four species of pulmonates – *Lymnaea columella*, *Helisoma duryi*, *Physa acuta* and *Aplexa waterloti*.

Two families, Thiariidae and Planorbidae, make up more than half (177 spp. or 60%) of the gastropod fauna of the Afrotropical Region; 50% (109 spp.) of the prosobranchs and 85% (64 spp.) of the pulmonates. These proportions vary slightly from those found for the basin as a whole – 60, 45 and 77% respectively. Between the two subfamilies of Planorbidae, the percentage of species in the Planorbinae are slightly less than expected (43% vs 54%) and the Buliniinae more than expected (57% vs 46%).

For the bivalves the superfamily Unionacea (15 species) is favoured over Sphaeriacea (12 species). Nevertheless, the Sphaeriacea are proportionally better represented than Unionacea in the basin. This may be related to their broader habitat tolerance.

8.4.2 **Gastropoda**

Subclass Streptoneura: The prosobranchs are most varied in the larger lakes and rivers of the continent which tend to be older and more stable bodies of water. Nevertheless, species are found in all classes of freshwater habitats.

The two species of Neritidae should be present in coastal areas adjacent to the mouth of the Zambezi as Azevedo *et al.* (1961) records both species to the north and south of this part of the river. *Neritina* are found in rivers and streams just above tidal influence and hardly penetrate inland. Littorinidae, another family of brackish (and marine) habitats, may be represented, as two species of *Littoraria* are known from Mozambique (Appleton 1996).

The Viviparidae are principally species of deep lakes and rivers. With the exception of the widespread species, *Bellamyia capillata* and the more restricted *B. monardi*, the remaining species are endemic to Lake Malawi. The Ampullariidae are adapted to seasonally flooded habitats as well as fast flowing streams and lake benthos. Again, it is the species found in seasonal habitats that are of wide distribution (i.e. *Lanistes ovum*, *Pila ovata*). The tropical African Hydrobiidae are poorly known (Brown 1994); most are associated with fast-flowing water in West Africa and the Congo Basin. The single (rare?) species from our region, *Lobogenes michaelis*, is the most widespread of this small genus as the other two species of the genus are found only in the upper reaches of the SE Congo basin.

The large family Bithyniidae is only represented by four species in our region, three so far known only as endemics with very restricted distributions (headwater streams in NE Zambia and Lake Malawi). Only *Gabbiella kisalensis* is widespread in a band across south-central Africa.

The Thiariidae, as elsewhere in Africa, are dominated by species endemic to the Great Lakes (i.e. the thalassoids of Lake Tanganyika). In our region it is the genus *Melanoides*, with nine endemic species adapted to the deep waters of Lake Malawi, that is prominent. The other melanoid, *M. tuberculata*, is successful in a wide diversity of habitats and is found in Asia and over much of tropical Africa. Two of the *Cleopatra* species seem to be restricted to the south-central band of Africa with *C. ferruginea* found throughout the eastern tropical areas of the continent.

Table 8.1. Systematic checklist of the freshwater molluscs found in the Zambezi Basin, including Lake Malawi. Species listed in the literature as being from Zambia or Zimbabwe, or from Ethiopia to South Africa but not specifically noted as being from the Zambezi Basin (i.e. possible species), are shown by an asterisk (*). Source of data given in r. hand column.

Notes: § – species believed to have been introduced in recent historical time

B – species found in fresh to brackish waters

E – strictly endemic species

SUBCLASS STREPTONEURA (PROSOBRANCHS)

Order Archaeogastropoda

Family Neritidae

*B *Neritina natalensis* Reeve, 1855

Brown 1994

*B *Neritina pulligera* (Linnaeus, 1767, *Nerita*)

Brown 1994

Order Mesogastropoda

Family Viviparidae

Bellamyia capillata (Frauenfeld, 1865, *Vivipara*)

Brown *et al.* 1992

E *Bellamyia ecclesi* (Crowley & Pain, 1964, *Neothauma*)

Mandahl-Barth 1972

E *Bellamyia jeffreysi* (Frauenfeld, 1865, *Vivipara*)

Mandahl-Barth 1972

Bellamyia monardi (Haas, 1934, *Viviparus*)

Brown *et al.* 1992

E *Bellamyia robertsoni* (Frauenfeld, 1865, *Vivipara*)

Mandahl-Barth 1972

Family Ampullariidae

E *Lanistes (Lanistes) nasutus* Mandahl-Barth, 1972

Mandahl-Barth 1972

Lanistes (Lanistes) neavei Melvill & Standen, 1907

Brown 1994

E *Lanistes (Lanistes) nyassanus* Dohrn, 1865

Mandahl-Barth 1972

E *Lanistes (Lanistes) solidus* Smith, 1877

Mandahl-Barth 1972

Lanistes (Meladomus) ellipticus von Martens, 1866

Azevedo *et al.* 1961

Lanistes (Meladomus) ovum Peters, 1845

Brown *et al.* 1992

Pila occidentalis (Mousson, 1887, *Ampullaria*)

Brown *et al.* 1992

* *Pila ovata* (Olivier, 1804, *Ampullaria*)

Brown 1994

Family Littorinidae

*B *Littoraria intermedia* (Philippi 1846, *Nerita*)

Appleton 1996

*B *Littoraria subvittata* Reid, 1986

Appleton 1996

Family Hydrobiidae

Lobogenes michaelis Pilsbry & Bequaert, 1927

Brown 1994

Family Bithyniidae

humerosa group

Gabbiella (Gabbiella) kisalensis (Pilsbry & Bequaert, 1927, *Bulimus*)

Brown *et al.* 1992

stanleyi group

E *Gabbiella (Gabbiella) balovalensis* Mandahl-Barth, 1968

Mandahl-Barth 1968b

E *Gabbiella (Gabbiella) stanleyi* (Smith, 1877, *Bythinia*)

Mandahl-Barth 1972

E *Gabbiella (Gabbiella) zambica* Mandahl-Barth, 1968

Mandahl-Barth 1968b

Family Thiaridae

Cleopatra elata Dautzenberg & German, 1914

Brown *et al.* 1992

Cleopatra ferruginea (I. & H.C. Lea, 1850, *Melania*)

Azevedo *et al.* 1961

Cleopatra nsendweensis Dupuis & Putzeys, 1902

Brown *et al.* 1992

Cleopatra smithi Ancey, 1906

Brown 1994

E *Melanoides magnifica* (Bourguignat, 1889b, *Nyassia*)

Mandahl-Barth 1972

E *Melanoides nodicincta* (Dohrn, 1865, *Melania*)

Mandahl-Barth 1972

E *Melanoides nyassana* (Smith, 1877, *Melania*)

Mandahl-Barth 1972

E *Melanoides pergracilis* (von Martens, 1897, *Melania*)

Mandahl-Barth 1972

E *Melanoides polymorpha* (Smith, 1877, *Melania*)

Mandahl-Barth 1972

E *Melanoides pupiformis* (Smith, 1877, *Melania*)

Mandahl-Barth 1972

E *Melanoides simonsi* (Smith, 1877, *Melania*)¹

Brown 1994

- E *Melanoides truncatelliformis* (Bourguignat, 1889, *Nyassomelania*) Mandahl-Barth 1972
Melanoides tuberculata (Muller, 1774, *Nerita*) Mandahl-Barth 1972
 E *Melanoides turritispira* (Smith, 1877, *Melania*) Mandahl-Barth 1972
Melanoides victoriae (Dohrn, 1865, *Melania*) Brown *et al.* 1992
 *B *Thiara amarula* (Linnaeus, 1758, *Helix*) Brown 1994

Family Potamididae

- *B *Cerithidea decollata* (Linnaeus, 1758, *Helix*) Brown 1994

SUBCLASS EUTHYNEURA (PULMONATES)

Order Basommatophora**Family Ellobiidae**

- *B *Melampus semiaratus* Connolly, 1912 Appleton 1996

Family Lymnaeidae

- *§ *Lymnaea columella* Say, 1817 Brown 1994
Lymnaea (Radix) natalensis Krauss, 1848 Azevedo *et al.* 1961

Family Ancyliidae

- * *Burnupia caffra* (Krauss, 1848, *Ancylus*) Brown 1994
Ferrissia burnupi (Walker, 1912, *Ancylus*) Gray 1980
Ferrissia connollyi (Walker, 1912, *Ancylus*) Gray 1980
Ferrissia junodi Connolly, 1925 Gray 1980
 E *Ferrissia victoriensis* (Walker, 1912, *Ancylus*) Brown 1994
 E *Ferrissia zambesiensis* (Walker, 1912, *Ancylus*) Brown 1994

Family Planorbidae

Subfamily Planorbinae

- Afrogyrus coretus* (de Blainville, 1826, *Planorbis*) Brown *et al.* 1992
Biomphalaria angulosa Mandahl-Barth, 1957 Brown 1994
Biomphalaria pfeifferi (Krauss, 1848, *Planorbis*) Brown *et al.* 1992
Biomphalaria rhodesiensis Mandahl-Barth, 1957 Mandahl-Barth 1957a
Ceratophallus natalensis (Krauss, 1848, *Planorbis*) Brown & M.-Barth 1973
Gyraulus costulatus (Krauss, 1848, *Planorbis*) Brown *et al.* 1992
 § *Helisoma duryi* (Wetherby, 1879, *Planorbis*) Frandsen & Madsen 1979
 * *Lentorbis carringtoni* (Azevedo *et al.*, 1961, *Segmentorbis*) Azevedo *et al.* 1961
Lentorbis junodi (Connolly, 1922, 1925, *Hippeutis*) Brown 1994
Segmentorbis angustus (Jickeli, 1874, *Segmentina*) Brown *et al.* 1992
Segmentorbis kanisaensis (Preston, 1914, *Segmentina*) Brown *et al.* 1992

Subfamily Bulininae

africanus group

- Bulinus africanus* (Krauss, 1848, *Physopsis*) Mandahl-Barth 1957b
Bulinus globosus (Morelet, 1866, *Physa*) Brown *et al.* 1992

truncatus/tropicus complex

- Bulinus depressus* Haas, 1936 Brown *et al.* 1992
Bulinus natalensis (Küster, 1841, *Physa*) Brown 1994
 E *Bulinus nyassanus* (Smith, 1877, *Physa*) Mandahl-Barth 1972
 E *Bulinus* near *nyassanus* (Smith, 1877, *Physa*)² Mandahl-Barth 1972
 E *Bulinus succinoides* (Smith, 1877, *Physa*) Mandahl-Barth 1972
Bulinus tropicus (Krauss, 1848, *Physa*) Brown *et al.* 1992
Bulinus truncatus (Audouin, 1827, *Physa*) Brown 1994

forskali group

- Bulinus canescens* (Morelet, 1868, *Physa*) Mandahl-Barth 1968b
Bulinus forskalii (Fhrenberg, 1831, *Isidora*) Brown *et al.* 1992
Bulinus scalaris (Dunker, 1845, 1853, *Physa*) Brown *et al.* 1992

reticulatus group

- Bulinus reticulatus* Mandahl-Barth, 1954 Mandahl-Barth 1957b

Family Physidae

Subfamily Physinae

*§ *Physa acuta* Draparnaud, 1805

Brown 1994

Subfamily Aplexinae

§ *Aplexa waterloti* (Germain, 1911, *Physa*)

Connolly 1939

CLASS BIVALVIA

Order Filibranchia**Family Mytilidae***B *Brachidontes virgiliae* (Barnard, 1964, *Musculus*)

Appleton 1996

Order Eulamellibranchiata

SUPERFAMILY UNIONACEA

Family Unionidae*Cafferia caffra* (Krauss, 1848, *Unio*)

Mandahl-Barth 1988

E *Coelatura hypsiprymna* (von Martens, 1897, *Unio*)³

Mandahl-Barth 1988

Coelatura kumenensis (Mousson, 1887, *Unio*)³*Coelatura mossambicensis* (von Martens, 1859, *Unio*)³

Mandahl-Barth 1988

E *Nyassunio nyassaensis* (Lea, 1864, *Unio*)

Mandahl-Barth 1988

Family Mutelidae*Aspatharia pfeifferiana* (Bernard, 1860, *Margaritana*)

Daget 1998

E *Aspatharia subreniformis* (Sowerby, 1867, *Anodon*)

Daget, 1998

Chambardia nyassaensis (Lea, 1864, *Spatha*)

Mandahl-Barth 1988

Chambardia petersi (von Martens, 1859, *Spatha*)

Mandahl-Barth 1988

Chambardia wahlbergi wahlbergi (Krauss, 1848, *Iridina*)

Mandahl-Barth 1988

Mutela alata (Lea, 1864, *Spatha*)

Mandahl-Barth 1988

Mutela mabilii (Rochebrune, 1886, *Mutelina*)

Appleton 1979

Mutela rostrata (Rang, 1835, *Iridina*)

Curtis 1991

E *Mutela zambesiensis* Mandahl-Barth, 1988

Mandahl-Barth 1988

Family Etheriidae* *Eheria elliptica* Lamarck, 1807

Mandahl-Barth 1988

SUPERFAMILY SPHAERIACEA

Family Corbiculidae*Corbicula astartina* (von Martens, 1859, *Cyrena*)

Mandahl-Barth 1972

Corbicula fluminalis africana (Krauss, 1848, *Cyrena*)

Mandahl-Barth 1972

Family Euperidae*Eupera ferruginea* (Krauss, 1848, *Cyclas*)

Mandahl-Barth 1972

* *Eupera ovata* (Mandahl-Barth, 1954, *Byssanodonta*)

Mandahl-Barth 1972

Family Sphaeriidae*Musculium incomitatum* (Kuiper, 1966, *Pisidium*)

Mandahl-Barth 1988

Pisidium kenianum Preston, 1911

Korniushin 1998

* *Pisidium ovampicum* Ancey, 1890

Mandahl-Barth 1988

Pisidium pirothi Jickeli, 1881

Mandahl-Barth 1972

Pisidium reticulatum Kuiper, 1966

Mandahl-Barth 1972

Pisidium viridarium Kuiper, 1956

Mandahl-Barth 1988

* *Sphaerium bequaerti* (Dautzenberg & German, 1914, *Eupera*)

Mandahl-Barth 1988

Sphaerium capense (Krauss, 1848, *Cyclas*)

Curtis 1991

¹ *Melanoides simonsi* may be a valid species (Brown 1994).² *Bulinus* near *nyassanus* may be a new species (Mandahl-Barth 1972, Wright *et al.* 1967).³ Appleton (1996) and Rosenberg *et al.* (1990), citing priority, use *Coelatura* rather than *Caelatura*.

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
Ampullariidae																		
<i>Pila occidentalis</i>		X	X															from W Zambia to S Angola & N Botswana
<i>Pila ovata</i>																		temporary pools, papyrus swamps, stony beaches
Littorinidae																		
<i>Littoraria intermedia</i>																		mangrove forest, saltmarsh
<i>Littoraria subvittata</i>																		mangrove forest, saltmarsh
Hydrobiidae																		
<i>Lobogenes michaelis</i>			X	X														streams over gravel, muddy pools, warm salt springs
Bithyniidae																		
<i>Gabbiella balovalensis</i>	X																	stream
<i>Gabbiella kisalensis</i>		X	X							X								streams over gravel, slow waters, floodplains
<i>Gabbiella stanleyi</i>								X										littoral zone 12-95m throughout L.Malawi
<i>Gabbiella zambica</i>									X									streams?
Thiaridae																		
<i>Cleopatra elata</i>		X	X				X											streams, rivers & floodplains
<i>Cleopatra ferruginea</i>																		ponds, streams, swamps, rocks in permanent rivers
<i>Cleopatra nsendweensis</i>																		rivers
<i>Cleopatra smithi</i>		X	X	X							X							rivers, streams
<i>Melanoides magnifica</i>																		only known from one location in L.Malawi
<i>Melanoides nodicincta</i>																		throughout W shore of L.Malawi, depths to 27m
<i>Melanoides nyassana</i>								X										only known from SE arm of L.Malawi
<i>Melanoides pergracilis</i>								X										throughout W shore of L.Malawi down to 27m
<i>Melanoides polymorpha</i>								X										throughout L.Malawi, lakeshore down to 4.5m
<i>Melanoides pupiformis</i>								X										throughout W shore of L.Malawi down to 21m
<i>Melanoides simonsi</i>								X										lake; only known from type locality

Family/species	Upper Zambezi					Middle Zambezi					Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/C	Kaf	Ban	other	MZV	CB	LM	other	L.Sh	Del	IOC	other				
<i>Melanoides truncatelliformis</i>								X								E		lake; only known from N end of L.Malawi
<i>Melanoides tuberculata</i>							X	X	X		X						X	permanent waters with abundant bottom sediments; brackish waters
<i>Melanoides turritispira</i>																E		throughout lake down to 5m
<i>Melanoides victoricae</i>		X							X								X	rivers with sand or mud bottoms, floodplains
<i>Thiara amarula</i>													?				X	coastal freshwater above tidal influence
Potamididae																		
<i>Cerithidea decollata</i>													?				X	brackish water, mangrove trunks
PULMONATES																		
Ellobiidae																		
<i>Melampus semiaratus</i>																	X	brackish water in mud under mangroves
Lymnaeidae																		
<i>Lymnaea columella</i>									X								X	Introduced; common in permanent streams, dams
<i>Lymnaea natalensis</i>		X	X		X		X	X	X		X		X				X	lakes, rivers, swamps, ditches. Pollution & desiccation-tolerant
Ancylidae																		
<i>Burnupia caffra</i>									?								X	V. variable sp.; stream shores & to 100m in lakes
<i>Ferrissia burnupi</i>										X							X	lakes, decaying plant stems below dam
<i>Ferrissia connollyi</i>											X						X	decaying plant stems at dam edge
<i>Ferrissia Junodi</i>																		decaying plant stems & submerged twigs in swamp
<i>Ferrissia victoriensis</i>																	E	rivers attached to vegetation
<i>Ferrissia zambesiensis</i>									X								E	rivers
Planorbidae																		
<i>Afrogynus coretus</i>		X	X						?								?	permanent waters with rich aquatic vegetation
<i>Biomphalaria angulosa</i>									X								X	seasonal swamps & irrigation schemes

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi			Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC				
<i>Biomphalaria Pfeifferi</i>	X	X	X	X	?	X	X	X	X	X	X	X	X	X	X	X	ditches, ponds, swamps, streams, irrigation channels
<i>Biomphalaria rhodesiensis</i>				X		X										X	lakes, hillside streams
<i>Ceratophallus natalensis</i>						X		X								X	marshes, slow streams, rain pools
<i>Gyraulus costulatus</i>		X	X			X	X				X					X	dams, lakes, aquatic vegetation, stones in slow flowing water
<i>Helisoma duryi</i>						X										X	Introduced; cooling ponds, reservoirs, pools, dams, rivers
<i>Lentorhis carringtoni</i>													X				aquatic vegetation in lakes, marshes, slowly flowing rivers
<i>Lentorhis junodi</i>											X	X			?	X	aquatic vegetation in marshes, slow-flowing rivers, streams, ponds
<i>Segmentorhis angustus</i>		X	X			X	X	X				X				X	vegetation in marshes, rocks in streams, puddles
<i>Segmentorhis kamisaensis</i>		X														X	permanent marshes, rain pools
<i>Bulinus africanus</i>				X	X	X	X				X	X				X	permanent streams, small dams
<i>Bulinus canescens</i>				X													marshes
<i>Bulinus depressus</i>		X	X		X											X	rivers, lakes, temporary marsh, reservoirs, dams
<i>Bulinus forskalii</i>				X		X	X	X		X	X	X				X	natural & artificial waters, flowing or stagnant
<i>Bulinus globosus</i>		X	X		X		X	X		X	X					X	streams, rivers, seasonal pools, aquatic plants in shallow water
<i>Bulinus natalensis</i>						X										X	small pools, slow flowing rivers, lakes
<i>Bulinus nyassanus</i>								X									coarse substrate on SW shore of L.Malawi at 1.5-15m; deep water form at 95m
<i>Bulinus nr. nyassanus</i>								X									deep water form dredged from 95m, SW shore of L.Malawi
<i>Bulinus reticulatus</i>				X		X	X										small briefly filled pools
<i>Bulinus scalaris</i>		X	X	X		X	X	X								X	seasonal pools lacking vegetation, floodplains
<i>Bulinus succinoides</i>								X									SW shore at 4.5m on Vallisneria aethiops plants

Family/species	Upper Zambezi					Middle Zambezi					Lower Zambezi			Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/C	Kaf	Ban	other	MZV	CB	LM	other	L.Sh	Del	IOC				
<i>Bulinus tropicus</i>	X	X	X	X		X	X			X					X		small earth dams, pools in seasonal streams
<i>Bulinus truncatus</i>								X							X		decaying vegetation in flowing to standing waters
Physidae																	
<i>Physa acuta</i>									X						?		Introduced. Stagnant & flowing water near towns
<i>Aplexa waterloti</i>							X										Introduced. Flowing & standing water modified by man
BIVALVES																	
UNIONACEA																	
Mytilidae																	
<i>Brachidontes virgillae</i>													?			X	brackish water, also fresh water
Unionidae																	
<i>Cafferia caffra</i>			X	X		X											lakes, rivers, puddles
<i>Coelatura hypsiptyma</i>									X								widespread in L. Malawi; sandy mud at 3-4.5m
<i>Coelatura kunenensis</i>	X	X	X	X		X									X		seasonally inundated area below perennial swamps in clay bottom
<i>Coelatura mossambicensis</i>							X	X		X						X	rivers, also lake bed. Common in L. Kariba
<i>Nyassunio nyassaensis</i>								X								E	sandy mud at 3-12m; widespread in L. Malawi
Mutelidae																	
<i>Aspatharia pfeifferiana</i>	X	X	X	X		X			X					X			lacustrine, clean sandy bottoms, high oxygen content
<i>Aspatharia subreniformis</i>										X						E	soft mud in shallow edges of river & lake at 4-12 m
<i>Chambardia nyassaensis</i>										X						X	lake, depth of 3-12m; widespread in L. Malawi & L. Tanganyika
<i>Chambardia petersi</i>							X	X								X	?
<i>Chambardia w. wahlbergi</i>	X	X	X	X		X		X	X								lacustrine, running water, ditches, small dams
<i>Mutela alata</i>																E	lakes, rivers, muddy environments

Family/species	Upper Zambezi						Middle Zambezi						Lower Zambezi			Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other					
<i>Mutela mabilli</i>	X	X	X				X										X	lakes, rivers, muddy pools	
<i>Mutela rostrata</i>		X	X				X										X	rivers	
<i>Mutela zambeziensis</i>			X				X										E	?	
Etheriidae																			
<i>Etheria elliptica</i>						X											X	rapids, rivers, lakes, marine?	
SPHAERICEA																			
Corbiculidae																			
<i>Corbicula astartina</i>					X		X	X									X	lakes, rivers	
<i>Corbicula fluminalis africana</i>		X	X				X	X									?	common in L. Malawi & other lakes	
Euperidae																			
<i>Eupera ferruginea</i>		X	X			X		X			X						X	rivers, lakes, small dams	
<i>Eupera ovata</i>									X								X	small lakes	
Sphaeriidae																			
<i>Musculium incomitatum</i>			X			X											X	small lakes, dams	
<i>Pisidium kenianum</i>									X								X	rivers	
<i>Pisidium ovampicum</i>																	X	mountain streams	
<i>Pisidium prothi</i>					X	X		X									X	lakes, rivers, canals, depth 9-12m; most common African <i>Pisidium</i>	
<i>Pisidium reticulatum</i>								X									X	lakes & rivers, depth 9-12m	
<i>Pisidium viridarium</i>					X	X			X								X	rivers	
<i>Sphaerium bequaerti</i>						X											X	rivers	
<i>Sphaerium capense</i>		X	X			X			X								X	rivers, small lakes, dams	
TOTALS	4	27	31	15	9	33	23	12	47	22	7	12	8	4	36	38	56		

Table 8.3. Comparison of the molluscan fauna of the Zambezi Basin with that of the continental Afrotropics (number of species). Introduced species, species with Palaearctic affinities and coastal/brackish water species are excluded. Percentages are given in brackets.

	non-endemic	endemic	totals
ZAMBEZI BASIN			
Gastropoda	40	23	63 (70)
Prosobranchs	15	18	33 (52)
Pulmonates	25	5	30 (48)
Bivalvia	22	5	27 (30)
Unionacea	10	5	15 (57)
Sphaeriacea	12	0	12 (43)
All Mollusca	62 (69)	28 (31)	90 (100)
AFROTROPICAL REGION			
Gastropoda	-	-	295 (76)¹
Prosobranchs	-	-	220 (75)
Pulmonates	-	-	75 (25)
Bivalvia	-	-	94 (24)²
Unionacea	-	-	65 (69)
Sphaeriacea	-	-	29 (31)
All Mollusca	-	-	389 (100)

Notes: ¹ Number of species of gastropods by subclass and family derived from Brown (1994, Table 2.1), although analysis is restricted to those families found in the Zambezi Basin.

² Number of species for bivalves derived from Daget (1998) and Mandahl-Barth (1972, 1988).

Subclass Euthyneura: The pulmonates are most abundant in the smaller water bodies, including seasonal rain pools, and many have very extensive distributions. *Lymnaea natalensis* (Lymnaeidae), is the most widely distributed freshwater snail in Africa, though few species of *Lymnaea* occur on the continent (Brown 1994). *L. columella*, introduced to South Africa more than 50 years ago, is now found in most of the countries of Central and East Africa. *Melampus semiaratus* (Ellobiidae) is restricted to brackish habitats along the coast of East and Southern Africa and is possibly found in the Zambezi Basin.

The Ancyliidae are listed as having "five plus" species in Africa by Brown (1994, Table 2.1). Within the text he lists 50 species in three genera: *Ancylus* (3 species), *Burnupia* (21 species) and *Ferrissia* (26 species). The species of *Burnupia* are considered highly uncertain with many founded on what Brown considers non-specific shell differences and most may be reduced to synonymy with *B. caffer*. Most species of *Ferrissia* are known only from the type locality and few are considered specifically distinct for similar reasons to *Burnupia*. On the other hand, the members of this genus are very small (5 mm diam.) and are likely to be overlooked. The specific diversity of these two genera await further investigation (Brown 1994) and it is quite possible that there are no more than one or two species of *Ferrissia* in the basin. Unusually, *Ferrissia* thrive in stagnant environments (Brown 1994).

Table 8.4. Systematic checklist of the freshwater molluscs of Lake Malawi and Upper Shire. Strictly endemic species are indicated by the letter E. Source of data given in column on right.

CLASS GASTROPODA	
SUBCLASS STREPTONEURA (PROSOBRANCHS)	
<u>Order Mesogastropoda</u>	
Family Viviparidae	
<i>Bellamyia capillata</i> (Frauenfeld, 1865, <i>Vivipara</i>)	Mandahl-Barth 1972
E <i>Bellamyia ecclesi</i> (Crowley & Pain, 1964, <i>Neothauma</i>)	Mandahl-Barth 1972
E <i>Bellamyia jeffreysi</i> (Frauenfeld, 1865, <i>Vivipara</i>)	Mandahl-Barth 1972
E <i>Bellamyia robertsoni</i> (Frauenfeld, 1865, <i>Vivipara</i>)	Mandahl-Barth 1972
Family Ampuliariidae	
E <i>Lanistes (Lanistes) nasutus</i> Mandahl-Barth, 1972	Mandahl-Barth 1972
E <i>Lanistes (Lanistes) nyassanus</i> Dohrn, 1865	Mandahl-Barth 1972
E <i>Lanistes (Lanistes) solidus</i> Smith, 1877	Mandahl-Barth 1972
<i>Lanistes (Meladomus) ellipticus</i> von Martens, 1866	Mandahl-Barth 1972
<i>Lanistes (Meladomus) ovum</i> Peters, 1845	Mandahl-Barth 1972
Family Bithyniidae	
<i>stanleyi</i> group	
E <i>Gabbiella (Gabbiella) stanleyi</i> (Smith, 1877, <i>Bythinia</i>)	Mandahl-Barth 1972
Family Thiaridae	
E <i>Melanoides magnifica</i> (Bourguignat, 1889, <i>Nyassia</i>)	Mandahl-Barth 1972
E <i>Melanoides nodicincta</i> (Dohrn, 1865, <i>Melania</i>)	Mandahl-Barth 1972
E <i>Melanoides nyassana</i> (Smith, 1877, <i>Melania</i>)	Mandahl-Barth 1972
E <i>Melanoides pergracilis</i> (von Martens, 1897, <i>Melania</i>)	Mandahl-Barth 1972
E <i>Melanoides polymorpha</i> (Smith, 1877, <i>Melania</i>)	Mandahl-Barth 1972
E <i>Melanoides pupiformis</i> (Smith, 1877, <i>Melania</i>)	Mandahl-Barth 1972
E <i>Melanoides simonsi</i> (Smith, 1877, <i>Melania</i>) ¹	Brown 1994
E <i>Melanoides truncatelliformis</i> Bourguignat, 1889	Mandahl-Barth 1972
<i>Melanoides tuberculata</i> (Muller, 1774, <i>Nerita</i>)	Mandahl-Barth 1972
E <i>Melanoides turritispira</i> (Smith, 1877, <i>Melania</i>)	Mandahl-Barth 1972
SUBCLASS EUTHYNEURA (PULMONATES)	
<u>Order Basommatophora</u>	
Family Lymnaeidae	
<i>Lymnaea (Radix) natalensis</i> Krauss, 1848	Mandahl-Barth 1972
Family Ancyliidae	
<i>Ferrissia burnupi</i> (Walker, 1912, <i>Ancylus</i>)	Gray 1980
<i>Ferrissia junodi</i> Connolly, 1925	Gray 1980
Family Planorbidae	
Subfamily Planorbinae	
<i>Biomphalaria angulosa</i> Mandahl-Barth, 1957	Brown 1994
<i>Biomphalaria pfeifferi</i> (Krauss, 1848, <i>Planorbis</i>)	Mandahl-Barth 1972
<i>Ceratophallus natalensis</i> (Krauss, 1848, <i>Planorbis</i>)	Mandahl-Barth 1972
<i>Gyraulus costulatus</i> (Krauss, 1848, <i>Planorbis</i>)	Mandahl-Barth 1972
<i>Segmentorbis angustus</i> (Jickeli, 1874, <i>Segmentina</i>)	Brown 1994

Subfamily Buliniinae

africanus group

<i>Bulinus globosus</i> (Morelet, 1866, <i>Physa</i>)	Mandahl-Barth 1972
<i>truncatus/tropicus</i> complex	
E <i>Bulinus nyassanus</i> (Smith, 1877, <i>Physa</i>)	Mandahl-Barth 1972
E <i>Bulinus</i> near <i>nyassanus</i> (Smith, 1877, <i>Physa</i>) ²	Mandahl-Barth 1972
E <i>Bulinus succinoides</i> (Smith, 1877, <i>Physa</i>)	Mandahl-Barth 1972
<i>Bulinus truncatus</i> (Audouin, 1827, <i>Physa</i>)	Gray 1984
forskalii group	
<i>Bulinus forskalii</i> (Ehrenberg, 1831, <i>Isidora</i>)	Mandahl-Barth 1972
<i>Bulinus scalaris</i> (Dunker, 1845, <i>Physa</i>)	Gray 1981a

CLASS BIVALVIA

Order Eulamellibranchiata

SUPERFAMILY UNIONACEA

Family Unionidae

E <i>Coelatura hypsiprymna</i> (von Martens, 1897, <i>Unio</i>) ³	Mandahl-Barth 1988
<i>Coelatura mossambicensis</i> (von Martens, 1859, <i>Unio</i>) ³	Mandahl-Barth 1988
E <i>Nyassunio nyassaensis</i> (Lea, 1864, <i>Unio</i>)	Mandahl-Barth 1988

Family Mutelidae

E <i>Aspatharia subreniformis</i> (Sowerby, 1867, <i>Anodon</i>)	Daget, 1998
<i>Chambardia nyassaensis</i> (Lea, 1864, <i>Spatha</i>)	Mandahl-Barth 1988
<i>Chambardia wahlbergi wahlbergi</i> (Krauss, 1848, <i>Iridina</i>)	Mandahl-Barth 1988
E <i>Mutela alata</i> (Lea, 1864, <i>Spatha</i>)	Mandahl-Barth 1988

SUPERFAMILY SPHAERIACEA

Family Corbiculidae

<i>Corbicula astartina</i> (von Martens, 1859, <i>Cyrena</i>)	Mandahl-Barth 1972
<i>Corbicula fluminalis africana</i> (Krauss, 1848, <i>Cyrena</i>)	Mandahl-Barth 1972

Family Euperidae

<i>Eupera ferruginea</i> (Krauss, 1848, <i>Cyclas</i>)	Mandahl-Barth 1972
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Family Sphaeriidae

<i>Pisidium pirothi</i> Jickeli, 1881	Mandahl-Barth 1972
<i>Pisidium reticulatum</i> Kuiper, 1966	Mandahl-Barth 1972

Notes:¹ *Melanoides simonsi* may be a valid species (Brown 1994).

² *Bulinus* near *nyassanus* may be a new species (Mandahl-Barth 1972, Wright *et al.* 1967).

³ Appleton (1996) and Rosenberg *et al.* (1990), citing precedence, use *Coelatura* rather than *Caelatura*.

Table 8.5. Comparison of the molluscan fauna of Lake Malawi (including Upper Shire River) with Lake Tanganyika (number of species). Percentages are given in brackets.

	non-endemic	endemic	total
LAKE MALAWI			
Gastropoda	16	19	35 (74)
Prosobranchs	4	16	20 (57)
Pulmonates	12	3	15 (43)
Bivalvia	8	4	12 (26)¹
Unionacea	3	4	7 (58)
Sphaeriacea	5	0	5 (42)
All Mollusca	24 (51)	23 (49)	47 (100)
LAKE TANGANYIKA			
Gastropoda	21	38	59 (82)²
Prosobranchs	8	37	45 (76)
Pulmonates	13	1	14 (24)
Bivalvia	4	9	13 (18)¹
Unionacea	2	8	10 (82)
Sphaeriacea	2	1	3 (18)
All Mollusca	25 (35)	47 (65)	72 (100)

Notes: ¹ Number of species for bivalves derived from Daget (1998) and Mandahl-Barth (1972, 1988).

² Number of gastropod species derived from Brown (1994, Table 12.10).

The Planorbidae are by far the largest family of pulmonates in the basin. Inhabitants of temporary water sites, the family is dominated by the genera *Bulinus* (13 species) and *Biomphalaria* (3 species), both in numbers of species and in distribution. The success of *Bulinus* may be attributed to its ability to aestivate for many months in dry mud. *Biomphalaria* has less ability in this regard and is perhaps less successful in the drier parts of Africa (Brown 1994). Of particular significance for both *Biomphalaria* and *Bulinus* is that they are the intermediate host of many species of *Schistosoma*. Of greatest concern by far are the species *S. mansoni* and *S. haematobium*, the causes of bilharzia throughout Africa. *Biomphalaria* is the most important vector of *S. mansoni* as all species have at least one compatible strain of the parasite (Brown 1994). *S. haematobium* is transmitted entirely by *Bulinus* spp., of which *B. africanus*, *B. globosus* and *B. truncatus* are particularly important.

The only planorbid species with a restricted range are the endemics of Lake Malawi (*Bulinus nyassanus*, *B. nr. nyassanus* and *B. succioides*) and *Biomphalaria angulosa*, *B. rhodesiensis* and *Lentorbis carringtoni*. The two *Biomphalaria* are found in southern Tanzania, southeast Congo, northeastern and central Zambia and Lake Malawi. *L. carringtoni* ranges through the coastal areas from Mozambique to Natal. The introduced species *Helisoma duryi* can now be found throughout Africa. Two species of Physidae were also probably introduced, but as the taxonomy of this family is unstable it is unclear how many species are present (Brown 1994).

Biomphalaria pfeifferi occurs in a great variety of habitats, including man-made ones such as irrigation channels, and the species is found from Arabia through tropical Africa. Its success seems to be limited along the east coast by high temperatures, and by low temperatures in the African "temperate" highlands (Brown 1994). It is the most important vector of *S. mansoni*.

The taxonomy of *Bulinus* is highly complex and species are not yet defined satisfactorily (Brown 1994, Brown & Rollinson 1996). The genus is normally divided into four groups based on shell characteristics, anatomy, chromosome number and molecular properties. These groups are *africanus*, the *truncatus/tropicus* complex, *forskalii* and *reticulatus*. All are represented in the basin. The genus is highly successful in small seasonal water bodies, though the Lake Malawi endemics are deep water species.

The *africanus* group includes *B. africanus* and *B. globosus*, the group with the greatest range of the genus in Africa. Both species are common in various natural and artificial situations, including lake margins, permanent swamps and irrigation systems, small water bodies that may be flowing or stagnant, perennial or temporary, and are sometimes polluted (Brown 1994).

The *truncatus/tropicus* complex is represented by seven species in the Basin, including the three endemics of Lake Malawi. Species are found in similar habitats to the *africanus* group. The *natalensis/tropicus* group is distributed along the east coastal third of Africa from Ethiopia to South Africa. However, there is some separation, possibly by temperature, between *B. natalensis* and *B. tropicus*, the latter associated with cooler and higher altitude environments than the former (Brown 1994). The distribution of *B. tropicus* is more equatorial, being found from East Africa through the Congo to most of tropical West Africa. An unusual feature of *B. truncatus* is its tetraploid chromosome composition. It is an extremely variable species and many named species have been synonymized with *B. truncatus*. Brown (1994) lists six of the most widely used names. Only *B. truncatus* of this complex is a natural vector of *S. haematobium*.

The *forskalii* group contains *B. canescens*, *B. forskalii* and *B. scalaris*, no species of which is a natural carrier of *S. haematobium* flukes. *B. forskalii* has an Afrotropical distribution, while *B. scalaris* is more limited to eastern, southern and south-central Africa. *B. canescens* is only found in central Angola, SE Congo and possibly central Zambia. Again, habitats are similar to other species of the genus.

The only representative of the *reticulatus* group is *B. reticulatus*, an inconspicuous species widely scattered in eastern and southern Africa. It is found in small rain pools and is not a natural host of *S. haematobium* (Brown 1994).

8.4.3 Bivalvia

Order Filibranchia: Only one Filibranchia is listed as a possible species for the Zambezi Basin. Appleton (1996) records *Brachidontes virgiliae* in the fresh to brackish waters on the coast of Mozambique to the Western Cape, but it has not been recorded from the basin.

Order Eulamellibranchiata: The remaining 27 bivalve species belong to the Eulamellibranchiata (mussels, clams and pill clams) and are true freshwater species. The systematics of this order is not satisfactory, although it was much improved by Mandahl-Barth's 1988 monographic treatment (see also Danish Bilharziasis Laboratory 1998). His reasons for the historical proliferation of described "species" and taxonomic chaos is as follows. Many inland waters are very isolated leading to genetic isolation of their bivalve fauna. There is a wide variety of biotopes which leads to new forms, i.e.

individuals adapt or perish. Yet such aquatic habitats are by nature unstable and of short duration, preventing the evolution of full new species. Consequently, the fauna has many forms at subspecific or variety level. Contributing to this often superficial variation in the Unionidae is their fertilisation and dispersal characteristics. There is no copulation, and fertilisation is external and accidental to some degree ensuring much crossbreeding. Dispersal of the parasitic larval stage is passive meaning that immature individuals, transported far from their place of origin, must adapt or perish. Much of this considerable adaptability is expressed in shell shape.

Superfamily Unionacea: This superfamily is represented in the basin by the families Unionidae, Mutellidae and possibly Etheriidae. The Unionidae (15% of the Afrotropical fauna) includes the widespread genera *Coelatura* (= *Caelatura*, Daget 1998, Rosenberg *et al.* 1990) and *Cafferia*. A third genus, *Nyassunio*, (considered by Mandahl-Barth (1972, 1988) as *Caelatura*) is found only in Lakes Malawi and Tanganyika. *Coelatura* is well known for its extreme plasticity of shell form which has led to approximately 200 supposed species or subspecies having been described in the past. Mandahl-Barth's (1988) analysis reduced these to no more than 24 species, two of them endemic to Lake Malawi and the Upper Shire River. More recently, Daget (1998) listed 28 valid species but under four genera, *Coelatura*, *Mweruella*, *Nitia* and *Nyassunio*. '*Coelatura*' (i.e. not in the strict sense of Daget) are principally species of large lakes and dams and perennial rivers. The remaining species, *Cafferia caffra*, is found throughout the southern part of the continent in smaller bodies of water. As with *Coelatura*, it is extremely variable in form.

The biggest bivalves, the Mutellidae, are better represented in the Zambezi region (around 23% of the Afrotropical fauna), including three endemics – *Mutela alata*, *M. zambesiensis* and *Aspatharia subreniformis*. However, as Mandahl-Barth (1988) points out, this family is rather confusing as it lacks useful taxonomic characters. Numerous species in the past have been based on the size, shape and thickness of the shell which he feels are of little specific value. He concludes by saying that it is impossible to decide how many species there are in Africa. *Aspatharia*, formerly a large genus of 34 species, has been reduced to 15, of which only two occur in our region (Daget 1998). *Chambardia* includes three of the seven species currently recognised out of the more than 50 described forms (Daget 1998). The genus is primarily an inhabitant of large lakes or dams. The taxonomy of the *Mutela* is difficult. Mandahl-Barth's (1988) attempt at unravelling the confusing taxonomic history of the genus is itself convoluted and confusing to a non-specialist. His admittedly unsatisfactory classification has reduced the plethora of named species (around 75) to a manageable 13. *Mutela* are large (100 mm) bivalves of both lakes and perennial rivers, and four species are found in the Zambezi Basin.

The last unionid family, the Etheriidae, is now considered to be represented in Africa by only one species, *Etheria elliptica*. It has not been specifically cited for our region, but as it is common and its distribution is noted to cover tropical Africa (Mandahl-Barth 1988), it is included in the checklist. Its preferred habitats are exposed rocky shores of great lakes and fast running rivers, rapids, cataracts and waterfalls, all of which are common in the basin.

Superfamily Sphaeriacea: This superfamily includes Corbiculidae, Euperidae (Korniushin 1998 *in lit.*) and Sphaeridae. All have representatives in the Zambezi Basin. Corbiculidae, the largest of the Sphaeriacea (generally 30 mm), contains only two species, *Corbicula astartina* and *C. fluminalis*. The latter originally was thought to represent at least 42 species (Mandahl-Barth 1988). Both occur over much of the continent in lakes and dams and the larger rivers. In our region, *C. fluminalis* is represented by the subspecies (or form) *africana*.

The two genera of Sphaeridae, *Sphaerium* (= ?*Musculium*, Korniusshin 1998 *in lit.*) and *Pisidium*, are tiny clams (12 mm and 5 mm respectively). They are found in all types of water bodies, often in very large numbers, and most species have very extensive distributions in Africa.

The last family, Euperidae, is often included in Sphaeridae and contains one small genus *Eupera*. Two species, *E. ferruginea* and *E. ovata*, occur over large portions of Africa. Azevedo *et al.* (1961) recorded *E.* (as *Byssanodonta*) *crassa* from central and coastal Mozambique. However, Daget (1998) considered this a mis-identification of *E. ferruginea*.

8.5 BIOGEOGRAPHY

8.5.1 Lake Malawi

Lake Malawi is of special significance within the Zambezi Basin. Its fauna (Table 8.4) is so distinct that biologically it has only a slight relationship to the rest of the basin. Non-endemics, with the exception of *Lanistes ellipticus* and *Biomphalaria angolensis*, are extremely widespread on the continent (i.e. *Bellamya capillata*, *Melanoides tuberculata*, *Lymnaea natalensis*, *Biomphalaria pfeifferi*, *Ceratophallus natalensis*, *Bulinus* spp., *Coelatura caffra*, *Chambardia wahlbergi*, *Corbicula fluminalis*, etc.).

The molluscs of Lake Malawi are often compared to those of the other Great Lake, Lake Tanganyika (Beadle 1981; Brown 1978, 1994). Table 8.5 summarises the fauna of the two lakes. While proportions of endemic gastropods are similar, Lake Tanganyika has a more diverse prosobranch assemblage, centred mainly around the unusual thalassoid group which includes a rich fauna of rocky shores. Like Lake Malawi, the species of pulmonates are similar in number (14-15) and most are of extremely widespread distribution.

A comparison of the bivalve richness is perhaps not valuable as the number of species indicated for Lake Tanganyika does not appear to be representative, particularly for the Sphaeriacea. What is significant is the proportion of endemics, which is considerably greater than that of Lake Malawi and again indicates the great age and stability of this deep lake. Lake Tanganyika also has two monotypic genera.

Since Lake Malawi is a deep, relatively stable environment of considerable age, why has there not been a speciation of the prosobranchs as found in Lake Tanganyika? Three reasons have been proposed. Firstly, Lake Malawi is somewhat younger and shallower than Lake Tanganyika and has been subject to more significant changes in water depth and, possibly, salinity (Lake Malawi, 1-2 million years BP, Fryer & Iles 1972; Lake Tanganyika, up to 6 million years BP, Brown 1994). Secondly, Lake Malawi has a very diverse snail-eating fish fauna that inhabits the rocky shoreline. Thirdly, the initial stock of Lake Malawi gastropods had different genetic characteristics (founder effect).

Owen *et al.* (1990) show that no more than 25,000 years ago, Lake Malawi was 250-300 m shallower than it is at present, and only 200 years ago the lake was 120 m lower than current levels. They claim that a large proportion of the *mbuna* rock-dwelling cichlid fish species would have had to evolve in this short period. Such fluctuations in water levels would certainly prove stressful on both fish and snail populations. However, such drastic changes would not take place 'overnight'. Both fish and snails should have been able to move vertically with the changing water levels as in

many places the shores of the lake are steep-sided with rocky habitats extending to considerable depths (Beadle 1981). Bowmaker *et al.* (1978) feel that large variations in lake level would have had little impact on cichlid biology but may have been of considerable importance for speciation. Brown (1994) notes that the two main isolating mechanisms proposed for Lake Tanganyika and other African Rift Valley lakes are (a) habitat fragmentation (e.g. the division of a rocky shoreline by the soft substrata of a river delta or sandy beaches), and (b) changes in lake level where populations evolve independently in separate small lakes while water level in the main basin is low. Both would have promoted speciation.

Fryer (1959) noted that Lake Malawi had a more diverse snail-eating fish fauna than Lake Tanganyika, while McKaye, Stauffer & Louda (1986) recorded more than a dozen molluscivorous fish species at Cape Maclear. Fryer proposed that it is these rock inhabiting fish that prevent snails from invading the rocky shoreline, but Beadle (1981) doubts this explanation. Yet in recent years the transmission of *Schistosoma haematobium* in tourist areas such as Cape Maclear has increased (Cetron *et al.* 1993) and it has been suggested that over-fishing of the snail-eating fishes may be the reason for the multiplication of the bilharzia snail vector *Bulinus globosus* (Cetron *et al.* 1996, Stauffer *et al.* 1997, but see Msukwa & Ribbink 1997).

Beadle (1981) makes a third and perhaps more significant point. Evolution works with the material available. The present prosobranch endemic array in Lake Malawi is clearly different from that found in Lake Tanganyika. Malawi's endemics occur in the genera *Bellamya*, *Gabbiella*, *Lanistes*, *Melanoides* and *Bulinus*. With the exception of one *Melanoides* species, the endemics of Tanganyika are derived from the thalassoid stock. Beadle suggests that of most importance was the peculiar genetic characteristics of the ancestral stock. Perhaps in Lake Malawi this stock could not evolve to forms adaptable to the rigorous conditions on wave-swept rocks.

8.5.2 Zambezi Basin

Pilsbry and Bequaert noted early in this century (1927) that the outstanding features of the freshwater molluscan fauna of the Afrotropical Region were its taxonomic poverty and uniformity over immense areas (c. 500 species, Brown 1994, Daget 1998, Mandahl-Barth 1988). While this is true for the pulmonates, and to some degree the bivalves (Appleton 1979, 1996), the prosobranchs show much more diversity with 'centres of endemism' in the Congo Basin, Lake Tanganyika, Lake Victoria and Lake Malawi. Nevertheless, species richness remains low relative to other invertebrate groups in Africa such as terrestrial snails (c. 5500 species, van Bruggen 1995) and insects (>1000 species of Odonata; >550 species of aquatic insects for Malawi alone, Dudley 1998). Although Pilsbry and Bequaert's point is certainly true, intriguing questions regarding speciation and biogeography remain (Brown 1994).

The Zambezi Basin mollusc fauna is clearly Afrotropical. Numerous species (i.e. *Melanoides tuberculata*, *Lymnaea natalensis*, *Gyraulus costulatus*, *Biomphalaria pfeifferi*, *Bulinus forskalii*, *Cafferia caffra*, *Pisidium pirothi* and *Chambardia wahlbergi*) extend far southwards well into Natal in South Africa through the 'tropical corridor' (Poynton 1964) along the eastern coastal areas of the continent. Many species reach their southern limits in the Pongola River region north of Natal, a major 'subtraction' zone (Brown 1994). Their southern geographical ranges show various degrees of restriction and they do not occur, or are sparsely represented, in the highlands of more equatorial latitudes, as seen in the genera *Biomphalaria* and *Bulinus*.

The southern limits of the fauna in the western and central parts of Africa lie at far lower latitudes, many species scarcely penetrating south of the Cunene and Okavango river systems and the Caprivi

Strip wetlands. For most species, aridity and, perhaps to a lesser degree, temperature may be the limiting factors (Brown 1994, Brown *et al.* 1992, Curtis 1991). Certainly the more narrowly tropical species of west and central tropical Africa (i.e. species of *Bellamya*, *Lanistes*, *Gabbiella*, *Cleopatra*, *Melanoides*, *Segmentorbis*, *Mutela* and *Sphaerium*) have the Zambezi River and the highlands of Zimbabwe as their southern limit. The Limpopo River valley has not provided western faunal elements access to Mozambique and the coastal corridor in recent geological time (Brown 1978).

The tropical molluscs categorised by Brown (1978) as broadly tropical include Zambezi Basin species such as *Melanoides tuberculata*, *M. victoriae*, *Lymnaea natalensis*, *Gyraulus costulatus*, *Ceratophallus natalensis*, *Biomphalaria pfeifferi*, *Bulinus africanus*, *B. forskalii*, *B. natalensis/tropicus*, *Physa acuta* and *Corbicula fluminalis africana*. These species have wider temperature tolerances and are able to live in both high cool and low warm tropical climatic conditions.

The gastropod faunas of Angola, Mozambique, Natal and East Africa are summarised in Table 8.6 and compared with that of the Zambezi Basin as a whole. It is clear that there are a small number of ubiquitous species (3 prosobranchs, 9 pulmonates) that occur over enormous geographical areas. Removing these species from the analysis gives a different picture. For the prosobranchs there is little significant overlap except for the Zambezi Basin with Mozambique and Angola. In fact, 12 of the 15 species of these two countries are found in the basin. The situation with the pulmonates is somewhat different. Shared species, notably over the 'base-line' number of nine, occur over a broad band of Africa from Angola to Mozambique as well as north to East Africa and south to Natal. A recent examination of the molluscs (gastropods and bivalves) of eastern Transvaal's Kruger National Park substantiates this similarity with 19 of its 21 indigenous species being found in the basin (De Kock & Wolmarans 1998).

It is perhaps more relevant to compare the freshwater mollusc species of the Zambezi Basin with those of the other three largest river basins in Africa – the Congo (Zaire), the Nile and the Niger.

8.5.3 The Congo Basin

The Congo River system has survived in its present state without great change at least through the Pleistocene. Much of the main river in the middle section of this basin was really almost lacustrine in character, similar to the great lake that occupied the basin during the Pliocene (Bailey 1986). The Luvua River tributary drains a huge area, much of this (the Luapula-Bangweulu-Chambeshi system or Zambia-Zaire (Congo) system of Bowmaker *et al.* 1978) probably captured from the Zambezi River. This system may have been the corridor by which Zambezi fish penetrated the Congo Basin as 18 species are shared solely by the two systems. However, Bell-Cross (1965a) found 16 species of fish in pools on the Muhinga watershed plain between the Zambezi and Congo systems (extreme NW Zambia) and points out that higher rainfall would have enabled these fish (and molluscs?) to move from one system to another. The present Congo is the seventh longest river in the world (4370 km) and has the second largest basin (4 million km²). Rainfall in the central basin occurs virtually throughout the year. Because the Congo straddles the equator and drains floodwaters alternately from north and south of the equator as the wet seasons change, fluctuations in water level are minimised ('reservoir' rivers) (Symoens *et al.* 1981).

8.5.4 The Nile Basin

The Sahara has long been the major hindrance to the movement of Afrotropical snails northward as well as Palaearctic species southward, and the connection of freshwater snail faunas of North Africa (Egypt) and tropical Africa is now restricted to the slender 6695 km thread of the Nile River.

Although certainly old in geological terms, the Nile has waxed and waned so frequently that, whenever time allowed an endemic fauna to evolve, a later recession largely destroyed it. Indeed the equatorial part of the Nile did not reach the Mediterranean until the mid-Pleistocene and may have ceased flowing on several occasions (Dumont 1986). The most recent 'last pluvial' occurred about 12,500 years BP (Beadle 1981) and it is during these periods of high water levels that faunal exchanges between central Africa, the Mediterranean and Asia must have occurred. The present basin (3 million km²) is a fairly homogeneous ecosystem except for the East African Great Lakes, and the fauna is overwhelmingly African (Dumont 1986).

Table 8.6. Comparison of the freshwater gastropods of the Zambezi Basin with those of Mozambique, Natal, Angola and East Africa (Tanzania, Uganda and Kenya). Introduced species, coastal/brackish water species and species endemic to Great Rift Valley lakes (i.e. Lake Malawi, Lake Tanganyika, Lake Victoria) are not included. *Burnupia* and *Ferrissia* are treated in the aggregate as genera. Figures are approximate and are derived from Brown (1978, 1994).

Geographical area	Total Species (no.)		
	Prosobranchs	Pulmonates	Total
Zambezi Basin (ZB)	17	23	40
Mozambique	9	13	22
Natal	5	18	23
Angola	11	16	27
East Africa	27	29	56
Species in Common (no./total no.)			
Mozambique/Natal	4/10	13/18	17/28
Mozambique/Angola	5/15	9/20	14/35
Natal/Angola	3/12	10/24	13/36
ZB/Mozambique	9/17	13/23	22/40
ZB/Natal	4/18	16/25	20/43
ZB/Angola	8/20	11/28	19/48
ZB/East Africa	5/39	20/32	25/71
Z/M/N/A/EA	3/43 (7%) ¹	9/39 (23%) ²	12/82 (14%)

Notes: ¹ *Bellamya capillata*, *Lanistses ovum* and *Melanoides tuberculata*.

² *Lymnaea natalensis*, *Burnupia* sp, *Ferrissia* sp, *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Segmentorbis kanisaensis*, *Bulinus africanus*, *B. globosus* and *B. forskalii*.

8.5.5 The Niger Basin

The "Nilotic" river basins of northern and western Africa, particularly the Nile and the Niger, have had geologically recent and substantial inter-connections (Beadle 1981). More humid conditions at the beginning of the Quaternary forced the proto-Upper Niger (then part of the Senegal River system) north to form an endorheic lake. Eventually this river was forced northeastwards where it broke through to join the Lower Niger. During this period there was an intermittent connection with Lake Chad, a connection which periodically still exists. Lake Chad was connected to the Nile through Bahr el Ghazal in recent prehistoric times (Beadle 1981, Welcomme 1986). The present Niger River is the third longest in Africa, yet it is poorly endowed with permanent tributaries as much of the river passes through very arid terrain (400 mm rainfall/year). Rainfall is seasonal over most of the 1.12

million km² basin and the resultant strong flood regime imposes an annual cycle of flood and drawdown that produces a constant but repetitive habitat instability ('pulse stable'). Water levels rise and fall sharply so that spates are of short duration and may occur a number of times a year. Such rivers are called 'sand bank' rivers (Symoens *et al.* 1981).

8.5.6 Comparison Between Basins

Table 8.7 provides a comparison of the freshwater snails of the Zambezi Basin with those of the Congo, Nile and Niger. Species from associated large lakes, coastal (brackish water) species, Palaearctic species and introduced species are not included.

The Congo system is the outstanding system for species richness (96 species) and endemics (60 species), particularly among the prosobranchs (74 and 57 species respectively). The Nile and Zambezi systems are a poor second and third in species richness and, like the Niger, very poor in endemics. Another notable feature is the high proportion of pulmonates in all three systems when compared to the Congo River. Only the Niger has fewer pulmonate species (14) than the Congo (22). The pulmonates of the Nile show the greatest richness (29 species) and endemism (6 species).

Table 8.7 also provides a comparison of the species found in common in the four river systems. The Congo system, being the geographically closest has the greatest species overlap with the Zambezi (29 species). A reasonable agreement is also seen between the Nile and the Zambezi (21 species). However, similarities with the Niger are probably near the minimal number found for any comparison between regions (12 species). For example, see the Natal, Mozambique, Angola and East African comparisons in Table 8.6. In fact, this value is identical to that of the four systems as a whole. Most of the species common between systems belong to the pulmonates, reaching 65% similarity for the Zambezi/Congo comparison.

The prosobranchs of the Zambezi River have no affinity with those of the Nile or the Niger River. Except for the extremely widespread *Pila ovata*, *P. wernei*, *Lanistes ovum* and *Melanoides tuberculata*, most prosobranchs are limited to a single river basin. The Congo River, which is believed to have captured some of the headwaters of the Upper Zambezi River, shows no more than a weak affinity, with 12 species in common. Three species, *Lanistes neavei*, *Lobogenes michaelis* and *Cleopatra smithi*, are only found in the Upper Zambezi and in the SE headwaters of the Congo. Two other species, *Lanistes ellipticus* and *Gabbiella kisalensis*, are found in the same two areas but have wider distributions, including the Middle Zambezi as well as southern Angola and the Caprivi/Okavango wetlands. The remaining seven species, *Bellamyia capillata*, *Lanistes ovum*, *Pila ovata*, *Cleopatra elata*, *C. ferruginea*, *C. nsendweensis* and *Melanoides tuberculata*, have much more extensive distributions.

The pulmonates show a much greater overlap between the river systems and geographical regions. This is undoubtedly related to their preference for shallow ephemeral bodies of water, their ability to aestivate and their high reproductive and dispersal powers. These are all characteristics which would favour pulmonate colonisation of the 'sandbank' rivers. Among the three basins, pulmonate richness and endemism seem, in part, to be related to basin size. Characteristic of the pulmonates' successful invasion of broad geographical areas is that no less than ten species of the total possible (32) are found in all four river systems (*Lymnaea natalensis*, *Burnupia* sp., *Ferrissia* sp., *Afrogyrus coretus*, *Gyraulus costulatus*, *Segmentorbis kanisaensis*, *Biomphalaria pfeifferi*, *Bulinus globosus*, *B. forskalii* and *B. truncatus*).

Table 8.7. Comparison of the freshwater molluscs of the Zambezi Basin with those of the Congo, Nile and Niger basins. Strictly endemic species from the Great Rift Valley lakes (i.e. Lake Malawi, Lake Tanganyika, Lake Victoria) and introduced species are not included. *Burmupia* and *Ferrissia* are treated in the aggregate as genera. Species endemic to the various basins are shown in brackets (E). All figures approximate and derived from Brown (1994), Daget (1998), Mandahl-Barth (1972, 1988).

Gastropoda	Total Species (no.)					
	<u>Prosobranchs</u>		<u>Pulmonates</u>		<u>Totals</u>	
	no.	end.	no.	end.	no.	end.
Congo (C)	74	57 (77)	22	3 (14)	96	60 (63)
Zambezi (Z)	17	2 (12)	23	0 (0)	40	2 (5)
Nile(N)	16	4 (29)	29	6 (21)	45	10 (22) ¹
Niger (Ni)	7	0 (0)	14	0 (0)	21	0 (0)
Bivalvia ²	<u>Unionacea</u>		<u>Sphaeriacea</u>		<u>Totals</u>	
	no.	end.	no.	end.	no.	end.
	Congo (C)	22	13 (59)	12	1 (8)	34
Zambezi (Z)	13	1 (8)	12	0 (0)	25	1 (4)
Nile (N)	10	0 (0)	8	1 (13)	18	1 (6)
Niger (Ni)	11	1 (9)	4	0 (0)	15	1 (7)
Gastropoda	Species in Common (no.)					
	<u>Prosobranchs</u>		<u>Pulmonates</u>		<u>Totals</u>	
	no.	%Pro	no.	%Pul	no.	%
Z/C		12	15	17	65	2928
Z/N		3	10	18	51	2132
Z/Ni	2	9	10	38	12	25
Z/C/N/Ni	2	2	10	26	12	9
Bivalvia	<u>Unionacea</u>		<u>Sphaeriacea</u>		<u>Totals</u>	
	no.	%Uni	no.	%Sph	no.	%
	Z/C		4	13	9	60
Z/N		3	15	5	33	823
Z/Ni	3	14	3	23	6	18
Z/C/N/Ni	2	5	3	17	5	8

Notes: ¹ The 8 Palearctic species indicated by Brown (1994, Table 12.16) are not included.

² Bivalve species with Palearctic affinities, coastal/brackish water species and the endemic species of Madagascar and associated islands are excluded.

Prosobranchs of African freshwater systems, like those of other continents, are more varied than the pulmonates (Brown 1994). Prosobranchs are more adapted to the relatively stable aquatic environments of deep lakes and large equatorial rivers (i.e. Lake Malawi, Congo River). Pulmonates, on the other hand, have difficulty invading deep water as most species need to regularly fill their lung with air. They also do not do well in turbulent rivers. Yet, being self-fertilising hermaphrodites, they have great reproductive powers and, consequently, are well adapted for dispersal to and colonisation of smaller, seasonal and, therefore, less stable water bodies. Such environments would not favour the evolution of new species. Any population developing specialised genotypic characteristics would not survive in the long run unless fortunate enough to be passively dispersed to a new favourable habitat. Under such conditions, more generalised characteristics with greater dispersal powers would be favoured.

A similar comparison of the bivalves (Table 8.7) supports this analysis. The Congo system remains the richest, although showing less dominance with a total of 34 species (14 endemic). The Zambezi system (25 species), the Nile (18 species) and the Niger (15 species) follow. What is remarkable is the almost complete lack of endemics in these three river basins. Another feature noted is the much higher proportion of the larger Unionacea relative to the smaller Sphaeriacea in the Congo and Niger systems (>60%) when compared to the other two basins (56 and 52%). The Unionacea make up 69% of the bivalves of the continent as a whole (Table 8.3). Again the Zambezi shares more species with the Congo (13) than with the Nile (8) or the Niger (6), and it is the Sphaeriacea which form the majority of them.

Thirty of the 41 species of the Unionacea mentioned here are confined to a single river system (although they may be present elsewhere), the exceptions being *Aspatharia pfeifferiana*, *Chambardia wahlbergi*, *Mutela mobilli*, *M. rostrata* and *Etheria elliptica*, the last two species occurring in all river basins. Like the pulmonates, the Sphaeriacea show the most overlap between geographical areas. Only seven species (41%) are limited to a single basin (again, they may occur elsewhere), while six species (*Corbicula fluminalis*, *Eupera ferruginea*, *Pisidium kenianum*, *P. pirothi*, *P. viridarium* and *Sphaerium hartmanni*) are found in three or more basins. Perhaps it is the superfamily's ecological versatility that provides the answer. However, it must be remembered that species delineation in bivalves is on the whole weaker than that of the gastropods, as is our knowledge of bivalve distributions. Therefore, the more conservative systematic treatment of Mandahl-Barth's (1988) has been used in the above analysis rather than that of Daget's (1998). Consequently, the results shown in Table 8.7 are very tentative.

The wide diversity of the Congo Basin mollusc fauna, particularly the prosobranchs, may be attributed to the great variety of habitats, the huge size of the system and its probable permanence and isolation through the Quaternary, first as a great lake and then as a river system. The Congo has been sufficiently isolated for a long enough time to evolve more endemic species than any other African water system. Of all the great basins it has been the least affected by earth movements or great climatic changes during the Pleistocene (Beadle 1981). In contrast, the other basins were being drastically altered by violent disruptive earth movements and fluctuations in climate (rainfall, surface water and temperature) (Welcomme 1986, Dumont 1986, Davies 1986, King 1978, Bowmaker *et al.* 1978), and this instability of 'sandbank' rivers continues today. Both the Nile and the Niger now flow through extremely arid regions. The area of the Middle and Lower Zambezi (before the large dams were built) was reduced to a fast flowing stream between rocks and sandbanks in the dry season. In flood, it overflowed and inundated large expanses of surrounding land. With respect to freshwater molluscs, environmental instability is a common feature of these three river systems, both over an evolutionary time scale and an annual time scale.

In conclusion, the Zambezi River system has a species richness considerably superior to the nearly equivalent sized Niger system. It is also slightly richer than the Nile with respect to Prosobranchs and Unionacea species numbers. Nevertheless, it is extremely poor in endemics and clearly Lake Malawi is the biodiversity heart of the basin. The high proportion of pulmonate (and Sphaeriacea?) species is to be expected as the stability and aquatic resources needed for prosobranch diversity are not available in the Zambezi system. Also expected, because of the pulmonates' preference for shallow unstable water bodies and their great ability to disperse and colonise such water bodies, is the uniformity of the species complexes over the four systems.

8.6 BIOMPHALARIA, BULINUS AND SCHISTOSOMIASIS

The driving force of modern malacology has been the importance of species of *Bulinus* and *Biomphalaria* as intermediate hosts of the serious human parasitic diseases – urinary (*Schistosoma haematobium*) and intestinal bilharzia (*S. mansoni*). After World War II, the World Health Organisation (WHO) and various national health authorities began to give serious consideration to the possible control of this blood fluke. This financial support and vigorous investigative effort has advanced knowledge for many species besides those of medical and veterinary importance.

Georg Mandahl-Barth, founder and first director of the Danish Bilharziasis Laboratory, has contributed many papers on mollusc biology, ecology and systematics including important regional faunas (Mandahl-Barth 1968a on SE Congo; 1972 on Malawi) and a comprehensive publication on the little-studied freshwater bivalves of Africa (Mandahl-Barth 1988). Others, such as C.A. Wright (1963, Angola, snails) and D. Brown *et al.* (1992, Namibia, snails; 1994, Africa, snails) of the Medical Research Council and the Biomedical Parasitology Section of the Natural History Museum in London, Azevedo *et al.* (1961, Mozambique, molluscs) of the Institute of Tropical Medicine in Lisbon, and C. Appleton (1979, south-central Africa, bivalves; 1996, southern Africa, molluscs) of the Department of Zoology and Entomology, University of Natal in South Africa, have provided comprehensive accounts of the molluscs of the Zambezi Basin as a direct outcome of their investigations of snails of medical importance. The most current information regarding the distribution of schistosomiasis (and consequently the snails *Biomphalaria pfeifferi* and *Bulinus africanus* and *B. globosus*) is the *Atlas of the Global Distribution of Schistosomiasis* (Doumenge *et al.* 1987), where each country is documented by text and maps.

Biomphalaria pfeifferi and *B. angulosus* are host to *S. mansoni*, although the latter species only occurs within the Zambezi Basin in Lake Malawi. However, the prevalence of *S. mansoni* is much less than that of *S. haematobium* in almost all areas. In Mozambique the highest rates occur near Tete (25%) with lower rates at Chinde (<1%), where population densities are too low to maintain significant infection foci points. Nearly 30% of all districts examined were without infection. In the past, prevalence rates were <10% in Malawi, even in the Southern Region. At present, rates vary between 20-30% with foci in the highlands overlooking the Shire Valley. The area of infection is increasing but rates remain about one third that of *S. haematobium*. Overall, more than half of the 524 bodies of water surveyed in the 1950s harboured *B. pfeifferi* in Mozambique and Malawi. The main endemic areas in Zimbabwe are in the northeast of the country with two-thirds of the population infected near the border with Zambia. The disease was seldom recorded in the drier northern Matabeleland. *B. pfeifferi* is ubiquitous in Zambia but the prevalence of intestinal bilharzia is very low (0-10%), being about one-fourth that of the urinary disease. Sturrock (1978, in Doumenge *et al.* 1987) points out two factors that seem to have a major influence on the distribution of the snail intermediate host in certain parts of the central plateau (1000-1300 m) with a continental climate. Low nocturnal temperatures limit the growth and life span of the snails and the water bodies, located on granite-based soils, have a low calcium and carbonate content which is unfavourable to the survival of *B. pfeifferi* and *Bulinus* spp. The most suitable areas are the flat valley bottoms with impeded drainage. Intestinal bilharzia and *B. pfeifferi* are found throughout the far upper reaches of the Kwando, Lungue Bongo and Luena Rivers in Angola and the Okavango and Chobe rivers in Namibia.

Bulinus africanus and *B. globosus* are the only known natural hosts of *Schistosoma haematobium* in the Zambezi Basin. According to Brown (1994), the most important and widespread of these is *B. globosus* as *B. africanus* inhabits the cooler climatic areas of southern Africa. Nevertheless, both

species are recorded as being hosts in areas of all countries that lie within the basin except Malawi (Brown 1994, Table 5.2) and Namibia (Brown *et al.* 1992), where *B. globosus* is the only species (but see Brown & Rollinson 1996).

Urinary bilharzia is endemic throughout the Zambezi Basin with prevalence rates reflecting human population densities and favourable snail habitats and transmission conditions. In Mozambique, *B. globosus* was ubiquitous and found in one third of all suitable sites examined; *B. africanus* being found in only 6%. Prevalence rates were high (80%) in the lower reaches of the Zambezi River as far as Chinde, but upstream at Tete rates decline (40-50%). Infection rates along the shores of Lake Malawi ranged from 30-50% with prevalence increasing southward reflecting increasing human densities. In the Lower Shire River Valley rates were extremely high at 90-95%. In Zimbabwe, prevalence rates tend to be higher in the wetter and cooler sites of the tributary headwaters of streams feeding the Zambezi River from the northern highlands. To the east in northern Matebeleland, infection rates are closer to 20% reflecting the drier conditions and sparse population. Infection rates appear to be lower in the sparsely populated districts of Zambia, being 5-10% in the Luangwa Valley and the Kafue River area, but reaching nearly 40% in the Zambezi headwaters in Northwest Province, the Gwembe Valley near Kariba and the Zambezi River. Significant infection rates persist into the upper reaches of the Zambezi in Angola and within the more southern Chobe/Caprivi wetlands of Namibia.

Notable *Bulinus* species absent from Brown's (1994) list of hosts of *S. haematobium* are *B. forskalii* and *B. tropicus*, both widely distributed species in Africa and in the Zambezi region. He points out that if the parasite were to evolve compatibility with these two common snails the prevalence of urinary schistosomiasis would be greatly increased.

8.7 CONSERVATION

The centre of molluscan endemism is Lake Malawi and, as such, it should be the focus of conservation concern. At present, the 1996 IUCN Red List of Threatened Animals lists eight species of gastropods from Lake Malawi as Vulnerable (*Bulinus nyassanus*) or Endangered (*Bellamya ecclesi*, *B. jeffreysi*, *B. robertsoni*, *Lanistes nasutus*, *L. nyassanus*, *L. solidus* and *Bulinus succinoides*, Baillie & Goombridge 1987). The criteria used were primarily based on the presence of small isolated fragmented populations and upon an assumed decline of various population parameters. All lake endemics are documented from small collections from only a few isolated lakeside localities; their actual distributions in the lake are unknown. These populations need further collection and analysis to establish their conservation status. Additionally, the doubtful specific status of *M. simonsi* and *B. nr. nyassanus* might be clarified through new collections. At present, the lakeshore and Upper Shire River environments have not been greatly affected by development and, without clear evidence to the contrary, these endemic populations would seem secure. Similar points could be made regarding the endemic bivalves *Coelatura hypsiprymna*, *Nyassunio nyassaensis*, *Chambardia nyassaensis* and *Mutela alata*.

Outside the Lake Malawi area, endemics include *Gabbiella stanleyi*, *G. zambica* and *Mutela zambesiensis*, the first two only known from their type localities (Chitipa, E Zambia and Mankoyo, NW Zambia respectively) and have not been collected since. Whether these three species are as strictly endemic as records indicate can only be determined by further investigations. If truly of such limited distribution, their survival would not be assured.

The only other species endemic to the basin, and of equally restricted distribution, are *Ferrissia victoriensis* and *F. zambesiensis*. However, endemism and rarity are unlikely. The genus is widespread in tropical Africa, but their shells are so small (2-6 mm dia) that these species are often overlooked (Brown 1994). The number of species is also uncertain as many were founded on shell differences, and few are likely to be distinct. Further study of *Ferrissia* (and *Burnupia*) is required to firmly establish the distinctness of the Ancyliidae species (Brown 1994).

8.8 FURTHER INVESTIGATIONS

Of the four principal wetlands of the Zambezi Basin, the Chobe/Caprivi area has been the most thoroughly studied (Brown *et al.* 1992, Curtis 1991, Curtis & Appleton 1987). Currently 20 species of gastropods have been identified from this wetland (Tables 8.2 and 8.8). With the exception of *Bellamya monardi*, which is restricted to the Cunene and Okavango river systems, all are widely distributed species of east, central and southern Africa. Brown *et al.* (1992) were disappointed to find no unique species in the Caprivi and they explained this finding in terms of hydrology and ecology. The Chobe/Caprivi watershed is poorly defined to the north east, allowing faunal exchange with a vast area of Central Africa. Also, without extensive stony rapids in the lower Okavango there is no 'high energy' niche which seems to have driven prosobranch speciation in West Africa. As noted earlier in this review, they found a considerable overlap (26%, 9 species) with the fauna of the Sudd region of the Nile (Brown *et al.* 1984), more than 3000 km to the north. Both lists were made up of snails that thrive in water bodies that are temporary to a greater or lesser degree and occupy seasonal water scattered over large areas of Africa. Curtis (1991) lists 11 species of bivalves from the Chobe/Caprivi wetlands, including only four Sphaeriacea. As with the gastropods, all except *Mutela zambesiensis*, which is endemic to the Central Zambezi, are found over considerable areas of east, central and southern Africa.

Table 8.8. Comparison of the published records of the molluscan fauna of four major wetland areas in the Zambezi Basin (number of species).

	Barotse floodplains	Chobe/ Caprivi	Lower Shire Valley	Zambezi Delta
Gastropoda				
Prosobranchs	n/a	9	n/a	7
Pulmonates	1	11	2	11
Subtotal	1	20	n/a	18
Bivalvia				
Unionacea	2	7	n/a	1
Sphaeriacea	n/a	4	n/a	2
Subtotal	2	11	n/a	3
Total	3	31	2	21

Note: Comparative data is scanty and should be treated with caution. There are no records available for some areas, particularly the Lower Shire.

The upper reaches of the Zambezi which extend into the south eastern areas of Angola were investigated by Wright many years ago (Wright 1963), and it would appear that there is much to learn about the molluscs of that vast country. The relatively ancient headwaters of the Zambezi to the north, associated with the Lungwebungo, Zambezi, Kabompo and Kafue Rivers, appear to have affinities with the moister Congo Basin, and may contribute new species. As Timberlake (1998) notes, it is here that both flora and fauna include genera and species more typical of the Congo Basin and species diversity for many groups is higher than elsewhere in the Zambezi Basin owing, in part, to it being a mixture of species from two regions.

The Barotse floodplains, the Busango and Lukango swamps and the Kafue floodplains are, except for isolated records, unknown as far as freshwater molluscs are concerned. However, because of the unstable hydrology characteristic of these regions, most species likely to be found would be widespread species similar to those found in the Chobe/Caprivi system.

The Lower Shire Valley wetlands have also not been studied systematically with regard to molluscs. As these marshes have a history of extreme instability and have been greatly modified by human activity, they are unlikely to include species of narrow distribution. Productive areas of investigation might be the rocky gorge environments of the Middle Zambezi and the Middle Shire, though again their relatively unstable aquatic environments would work against any unique forms.

Azevedo *et al.*'s (1961) survey of Mozambique, though now rather dated, forms the basis of what we know about the Zambezi Delta wetlands. For similar reasons to those proposed above, future studies of this region are unlikely to uncover new species, but will probably provide new records of freshwater/tidal interface species which are known to occur north or south of the delta (Neritidae, Assimineidae, Elloblidae and Mytilidae). The bivalves are essentially unknown, though again there should be no surprises within the strictly freshwater families.

An area of potential interest, but not strictly part of the present Zambezi River system, is the Chambeshi River/Bangweulu Lake/Luapula River system (The Zambia/Zaire [Congo] System of Bowmaker *et al.* 1978). The Luapula River, after passing over the Johnston and Mumbatuta Falls, enters Lake Mweru which ultimately drains into the Luvua River, a major tributary of the Lualaba and Congo Rivers. In 1948 Schwetz and Dartevelle published the first comprehensive analysis of the freshwater molluscs of this area, recording 33 species of which ten were considered endemic. The vast collections of L. Stapper, made just prior to the First World War, formed the basis of this study. Twenty years later Mandahl-Barth (1968a) reviewed the molluscs of this region and his results, based on a slightly larger geographical area (including the smaller bodies of water just to the east, which he called High Katanga, and west of the Luapula River), and a more current taxonomy, listed 72 species, 22 being endemic or near endemic. The current list of recognised species (Table 8.9), based on the recent works of Brown (1994) and Daget (1998), includes 71 species. Nineteen of these are endemic if the Upper Lufira River of Mandahl-Barth's High Katanga is included.

Perhaps 1 million years BP, the Luapula River, above the Johnston and Mumbatuta Falls, is thought to have captured the Chambeshi River in the vicinity of the Bangweulu Swamps (Thomas & Shaw 1988). The molluscan fauna provides some negative support for this idea. Except for two endemics of Lake Mweru, *Cleopatra smithi* and *C. johnstoni*, which also occur in the Luapula River just above Johnston Falls, and *Ferrissia zambiensis* which is doubtfully endemic (see Brown 1994), the Chambeshi River/Bangweulu Lake region does not contain any unique snail species or snail species with Congo affinities. Of the 24 species known from this system, 21 are widespread and found in

the Zambezi Basin. However, one endemic bivalve, *Coelatura choziensis*, is present in Lake Bangweulu as is a derived form (*schomburgki*) of *Mutela h. hageri*, an endemic of Lake Mweru. A second endemic, *Coelatura luapulaensis*, is found in the middle Luapula River below the lake but above the falls. Ten of the remaining 14 bivalves are also found in the Zambezi Basin. Lake Bangweulu and associated swamps are considered unproductive and with limited habitat diversity by Bowmaker *et al.* (1978) and may not be very old.

Table 8.9. Systematic checklist of the freshwater molluscs found in the Lake Mweru/Luapula River/Lake Bangweulu/Chambeshi River system (Zambian/Congo System) and "High Katanga", based on Brown (1994) and Mandahl-Barth (1968a, 1988).

- Notes: E - species endemic to this greater region
 § - species believed to have been introduced in recent historical time
- Columns: B - Chambeshi River/Lake Bangweulu, Upper Luapula region (above Johnston Falls)
 M - Lower Luapula River/Lake Mweru region
 K - "High Katanga" (middle and upper Lufira River and area near Lubumbashi)
 ? - Presence questioned by Mandahl-Barth (1968a)

CLASS GASTROPODA				
SUBCLASS STREPTONEURA (PROSOBRANCHS)				
<u>Order Mesogastropoda</u>				
	<u>B</u>	<u>M</u>	<u>K</u>	
Family Viviparidae				
	●	●		
E <i>Bellamya capillata</i> (Frauenfeld, 1865, <i>Vivipara</i>)				
E <i>Bellamya contracta</i> (Haas, 1934, <i>Vivipara</i>)			●	
E <i>Bellamya crawshayi</i> (Smith, 1893, <i>Viviparus</i>)		●		
E <i>Bellamya mweruensis</i> (Smith, 1893, <i>Viviparus</i>)		●		
E <i>Bellamya pagodiformis</i> (Smith, 1893, <i>Viviparus</i>)		●		
Family Ampullariidae				
<i>Lanistes (Lanistes) neavei</i> Melvill & Standen, 1907				●
<i>Lanistes (Meladomus) ellipticus</i> von Martens, 1866				●
<i>Lanistes (Meladomus) ovum</i> Peters, 1845	●	●		●
<i>Pila ovata</i> (Olivier, 1804, <i>Ampullaria</i>)				?
Hydrobiidae				
<i>Lobogenes michaelis</i> Pilsbry & Bequaert, 1927				●
<i>Lobogenes spiralis</i> Pilsbry & Bequaert, 1927				●
Bithyniidae				
<i>humerosa</i> group				
<i>Gabbiella kisalensis</i> (Pilsbry & Bequaert, 1927, <i>Bulimus</i>)	●			●
Thiaridae				
E <i>Cleopatra johnstoni</i> Smith, 1893	●	●		
E <i>Cleopatra mweruensis</i> Smith, 1893		●		
<i>Cleopatra nsendweensis</i> Dupuis & Putzeys, 1902		●		●
E <i>Cleopatra obscura</i> Mandahl-Barth, 1968				●
E <i>Cleopatra smithi</i> Ancey, 1906	●	●		
<i>Melanoides anomala</i> (Dautzenberg & Germain, 1914, <i>Melania</i>)				●
E <i>Melanoides crawshayi</i> (Smith, 1893, <i>Melania</i>)		●		
E <i>Melanoides imitatrix</i> (Smith, 1893, <i>Melania</i>)		●		
E <i>Melanoides mweruensis</i> (Smith, 1893, <i>Melania</i>)		●		

SUBCLASS EUTHYNEURA (PULMONATES)

Order Basommatophora

	<u>B</u>	<u>M</u>	<u>K</u>
Family Lymnaeida			
<i>Lymnaea (Radix) natalensis</i> Krauss, 1848	●	●	●
§ <i>Lymnaea (Radix) columella</i> Krauss, 1848			?
Family Ancyliidae			
<i>Burnupia caffra</i> (Krauss, 1848, <i>Ancylus</i>)	?	?	●
E <i>Burnupia kimiloloensis</i> Pilsbry & Bequaert, 1927			●
<i>Burnupia mooiensis</i> (Walker, 1912, <i>Ancylus</i>)			●
<i>Ferrissia fontinalis</i> Mandhal-Barth, 1968			●
E <i>Ferrissia zambiensis</i> Mandhal-Barth, 1968	●		
Family Planorbidae			
Subfamily Planorbinae			
<i>Afrogyrus coretus</i> (de Blainville, 1826, <i>Planorbis</i>)	?		●
<i>Biomphalaria angulosa</i> Mandahl-Barth, 1957	●		
<i>Biomphalaria pfeifferi</i> (Krauss, 1848, <i>Planorbis</i>)	●	●	●
<i>Biomphalaria rhodesiensis</i> Mandahl-Barth, 1957	●		
<i>Biomphalaria sudanica</i> (von Martens, 1870, <i>Planorbis</i>)	●		
<i>Ceratophallus natalensis</i> (Krauss, 1848, <i>Planorbis</i>)	●		
<i>Gyraulus costulatus</i> (Krauss, 1848, <i>Planorbis</i>)	●		●
<i>Lentorbis junodi</i> (Connolly, 1912, <i>Hippeutis</i>)	?		
<i>Segmentorbis angustus</i> (Jickeli, 1874, <i>Segmentina</i>)	●		●
<i>Segmentorbis excavatus</i> Mandahl-Barth, 1968			●
Subfamily Bullininae			
<i>africanus</i> group			
<i>Bulinus africanus</i> (Krauss, 1848, <i>Physopsis</i>)	●		
<i>Bulinus globosus</i> (Morelet, 1866, <i>Physa</i>)	●	●	●
<i>truncatus</i> / <i>tropicus</i> complex			
<i>Bulinus natalensis</i> (Kuster, 1841, <i>Physa</i>)	●		●
<i>Bulinus tropicus</i> (Krauss, 1848, <i>Physa</i>)	●	●	●
<i>Bulinus truncatus</i> (Audouin, 1827, <i>Physa</i>)			●
<i>forskalii</i> group			
<i>Bulinus canescens</i> (Morelet, 1868, <i>Physa</i>)			●
<i>Bulinus forskalii</i> (Ehrenberg, 1831, <i>Isidora</i>)	?	?	●
<i>Bulinus scalaris</i> (Dunker, 1845, 1853, <i>Physa</i>)	●		●
<i>reticulatus</i> group			
<i>Bulinus reticulatus</i> Mandhal-Barth, 1954	?		
Family Physidae			
Subfamily Physinae			
§ <i>Physa acuta</i> Draparnaud, 1805			?

CLASS BIVALVIA

Order Eulamellibranchiata

SUPERFAMILY UNIONACEA

Family Unionidae

E <i>Coelatura choziensis</i> (Preston, 1910, <i>Unio</i>) ¹	●		
E <i>Coelatura gabonensis</i> (Küster, 1862, <i>Unio</i>) ¹		●	
E <i>Coelatura kipopoensis</i> Mandahl-Barth 1968 ¹			●
E <i>Coelatura luapulaensis</i> (Preston, 1913, <i>Unio</i>) ¹	●		●
E <i>Mweuruella mweruensis</i> (Smith, 1908, <i>Unio</i>)		●	
E <i>Prisodontopsis aviculaeformis</i> Woodward, 1991		●	

Family Mutelidae

<i>Aspatharia pfeifferiana</i> (Bernardi, 1860, <i>Margaritana</i>)	●	●	●
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	<u>B</u>	<u>M</u>	<u>K</u>
<i>Chambardia dautzenbergi</i> (Haas, 1936, <i>Aspatharia</i>)	●		●
<i>Chambardia rubens rubens</i> (Cailliaud, 1823, <i>Anodonta</i>)	●	●	●
E <i>Mutela hargerii hargerii</i> Smith, 1908		●	
E <i>Mutela hargerii schomburgki</i> Haas, 1936	●		
<i>Mutela rostrata</i> (Rang, 1835, <i>Iridina</i>)		●	
Etheriidae			
<i>Etheria elliptica</i> Lamarck, 1807	●	●	●
Euperidae			
<i>Eupera ferruginea</i> (Krauss, 1848, <i>Cyclas</i>)	●	●	●
SUPERFAMILY SPHAERIACEA			
Family Corbiculidae			
<i>Corbicula africana</i> (Krauss, 1846, <i>Cyrena</i>)	?	●	?
<i>Corbicula astartina</i> (von Martens, 1859, <i>Cyrena</i>)	●		
Family Sphaeriidae			
<i>Musculium hartmanni bangweolicum</i> Haas, 1936	●		●
<i>Musculium incomitatum</i> (Kuiper, 1966, <i>Pisidium</i>)	●		●
<i>Pisidium kenianum</i> Preston, 1911			●
<i>Pisidium langleyanum</i> Melvill & Ponsonby, 1891	●		
<i>Pisidium priothi</i> Jickeli, 1881	●		
<i>Pisidium viridarium</i> Kuiper, 1956	●		
<i>Sphaerium bequaerti</i> (Dautzenberg & Germain, 1914, <i>Eupera</i>)	●	●	
<i>Sphaerium</i> (or <i>Musculium?</i>) <i>capense</i> (Krauss, 1848, <i>Cyclas</i>)	●		●

¹ Appleton (1996) and Rosenberg *et al.* (1990), citing precedence, use *Coelatura* rather than *Caelatura*.

On the other hand, Lake Mweru and the lower Luapula, separated from the Chambeshi River/Lake Bangweulu region by the two waterfalls and never thought to have been part of the Zambezi River system, have a relatively large number of endemic snails (10 species, prosobranchs: *Bellamya* (3), *Cleopatra* (4), *Melanoides* (3)) and bivalves (3 species, Unionacea: *Mweruella* (1), *Prisodontopsis* (1), *Mutela* (1)) more characteristic of the Congo system. Still, 16 of the 29 species known from this region are found in the Zambezi Basin. Schwetz and Darteville (1948) describe the present physiographic and bathymetric characteristics of Lake Mweru and the Lower Luapula River in some detail. However, as Brown (1994) points out, Lake Mweru must have been much deeper to have existed long enough to develop such a distinct assemblage, and both the lake and its molluscs now seem to be near the end of their life.

8.9 CONCLUSIONS

Freshwater molluscs do not really seem very useful in understanding changes in biodiversity across the Zambezi Basin. There are few, if any, endemics in this large area except for the isolated, ancient and stable habitat of Lake Malawi. However, among basins such knowledge may provide a measure of the stableness of the aquatic regime over geological time. Most of the major river basins of the continent have similar evolutionary histories in this regard and consequently very similar faunas. The exception is the Congo. What can be said is that the biodiversity of these aquatic organisms, whether unique or not, reflects the quality of the wetland ecosystem. In other words, a "full" mollusc

faunal complement at one site, even if nearly the same as at other sites, would suggest an aquatic ecosystem in reasonable shape and supportive of a full community of other aquatic invertebrates.

As Brown (1994) pointed out at the close of his introduction to his book, *Freshwater Snails of Africa and their Medical Importance*, a rich mollusc fauna is usually a sign of a healthy and sustainable aquatic ecosystem and it is the uncontaminated water from such systems on which the well-being of rural African communities depend.

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CHAPTER 9

REVIEW OF ODONATA ASSOCIATED WITH THE WETLANDS OF THE ZAMBEZI BASIN

Moira FitzPatrick

9.1 INTRODUCTION

With the increase in demand for arable land, the wetlands of the Zambezi Basin are under threat. In order to preserve these ecosystems an understanding of the biodiversity is important. Odonata are reliable indicators of the condition of aquatic and terrestrial ecosystems and are also ecologically important as they are major predators in these systems. Odonata are also relatively easily caught and are therefore ideal for monitoring changing conditions in the Zambezi wetlands. Although the Odonata, a primitive and ancient group of insects, are better documented than most invertebrate groups, it is unfortunate that data from the Zambezi Basin are scattered throughout many publications and hence this report is a consolidation of previous work in the basin, with particular reference to the Barotse floodplains, the Okavango Delta, the Lower Shire wetlands and the Zambezi Delta, highlighting shortcomings of the available data. Potential threats and conservation of Odonata populations are highlighted.

The Odonata are familiar insects in aquatic environments as they depend on water for most of their life cycle. In southern and central Africa the order Odonata consists of two suborders – the Anisoptera, or dragonflies, and the Zygoptera, or damselflies (Figure 9.1). The Anisoptera are stronger fliers and more robust than the more delicate Zygoptera. The more powerful fliers are capable of long sustained flight and thus adults are liable to spread further afield. This is evident in the Zambezi basin where 92 of the species collected are widespread throughout the Afrotropical region (Africa south of the Sahara) compared to 43 which have localised (limited) distributions (see Table 9.1). Some of the Anisoptera even extend their range to other continents such as *Pantala flavescens* to Europe, Asia, Australia and America and *Paragomphus genei* to Europe. In general, the Zygoptera, with their weak flying ability, tend to be more localised, e.g. *Lestes amicus* and *Pseudagrion assegaii*; of the 75 species found in the Zambezi Basin 31 are localized. *Agriocnemis exilis*, although the smallest and most delicate species, has a wide distribution throughout Africa as the adults are wafted from place to place by air currents.

The distribution of the Odonata is largely governed by the physical and vegetational conditions of the water and the nature of the substrate (Pinhey 1978). The structure of the vegetation, more than its composition, is significant to these predatory insects, providing perches for adults and, in certain genera, providing sites for egg laying and nurseries. More importantly, the vegetation provides shade and thus has an effect on the water temperature and microclimate, which together with salinity and strength of currents, control diversity of Odonata. Many species favour open stagnant pools, pans or swamps. Others prefer flowing streams, some hover over waterfalls, while there are those which are only found in the diffuse light of pools or slow moving streams which are well shaded with trees. Many species, however, are more tolerant of a wider range of conditions (eurytopic) and they are more widely distributed throughout southern and central Africa.

Figures 9.1; 9.2 and 9.3

Figure 1a: Anisoptera adult.

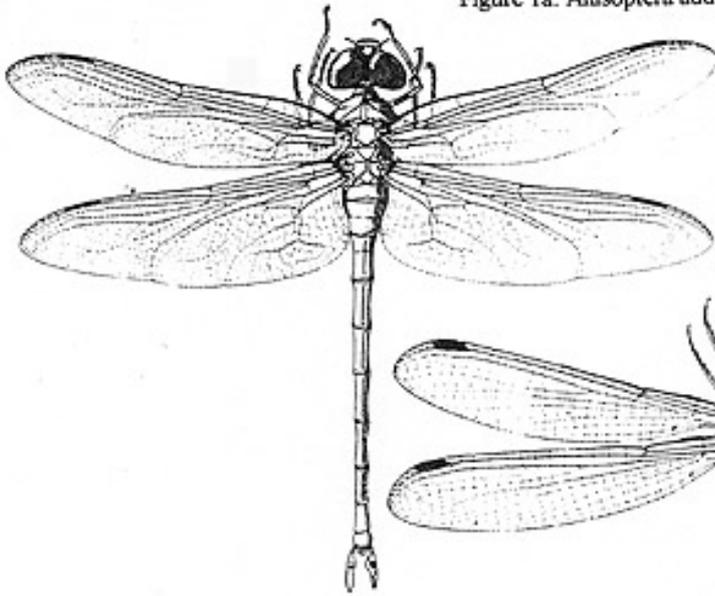


Figure 1b: Zygoptera adult.

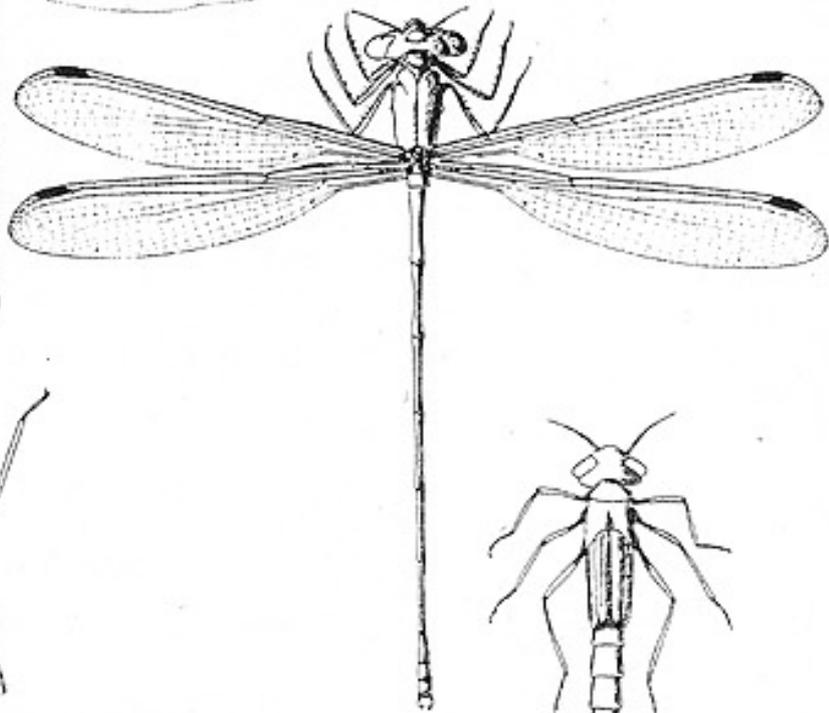


Figure 2a: Anisoptera larva.

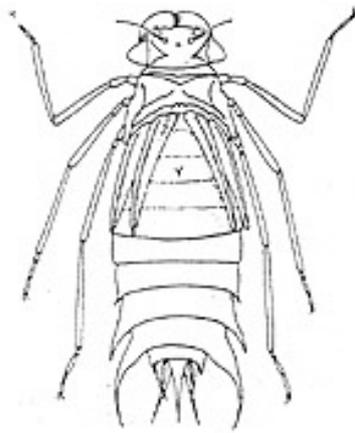


Figure 2b: Zygoptera larva.

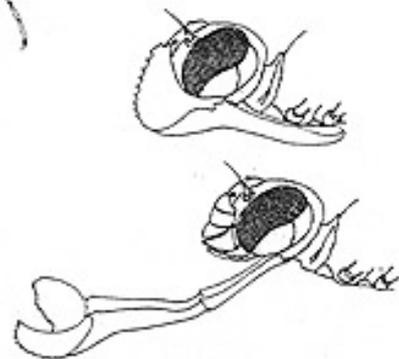


Figure 3: Mask (prehensile labium) of larva in retracted and extended position.

9.2 PREVIOUS WORK

Although the Odonata are abundant throughout the Zambezi Basin, especially in the wetlands, there has been little work done on the group. Sporadic collecting in the basin was done by Elliot Pinhey and this work resulted in taxonomic revisions and checklists published between 1950 and 1982, but little collecting has been done since then. Pinhey's collecting trips included the Mwinilunga district, Zambia in 1963, 1965 and 1972 (148 species recorded); a number of collecting expeditions to the Okavango and Chobe swamps during the years 1967-1976 (84 species recorded); various trips to Victoria Falls and Katombora between 1953 and 1963; trips to northern Malawi via Mpatamanga gorge along the lower Shire River (30 species recorded) in 1966 and 1970. He also collected in Mozambique between 1947 and 1973, but there are very few records (18 species) from the Zambezi Delta area. However, a recent collecting trip carried out under the Wetlands Biodiversity Assessment project increased the number of species to 31. Recent collecting also carried out under this project in March/April 1999 increased the number of species known from there from 5 to 33 (26 Anisoptera and 7 Zygoptera). Many of the earlier specimens are housed in the Natural History Museum, Bulawayo and form the basis of the attached checklist. All the specimens collected up to 1980 were identified by Pinhey, and are included in his publications. The only ecological work undertaken on the basin was carried out along Lake Kariba by Balinsky (1967) and is discussed below.

9.3 LIFE CYCLE

The adults of both suborders are insect predators which catch prey on the wing. Their legs are well developed, and situated in a forward position for catching and holding prey, and also for perching. Adults are diurnal and prefer warm areas, and males may display territorial behaviour. After mating, female Anisoptera generally lay their eggs directly into the water, tapping its surface with their abdomens to help withdraw the protruding eggs from their genital pores after which the eggs sink slowly to the bottom. Female Aeshnidae (Anisoptera) and Zygoptera have a spiny, sheathed ovipositor with which they make a number of slits in plant stems, either above or below the surface of the water, where they lay their eggs. The larvae, or nymphs, (Figure 9.2) are predators, feeding on invertebrates and small fish which they seize by shooting out the long prehensile labium (Figure 9.3). Some larvae live in mud, debris or among stones, while others are active scramblers amongst aquatic plants. Mature larvae climb up grass or reed stems, tree trunks, branches or rocks, until they are at or above the surface of the water, where they shed their last skin to become soft, teneral adults (newly emerged adults without full colouration and hardening of the cuticle). As soon as they are capable of flight they seek shelter and rest until their wings and body have hardened.

9.4 CONSERVATION AND POTENTIAL THREATS

Balinsky's (1967) work is the only ecological study of Odonata in the Zambezi Basin, but some work has been done around Pietermaritzburg and Kruger National Park, South Africa. The results of these studies are similar to those done elsewhere and are used as a basis for this discussion.

Savanna rivers, including the Zambezi, have variable water flows due to seasonal rainfall and drought, and any slight fluctuation in flow rates causes changes in the biotope (Stewart & Samways 1998). This causes a high turnover of Odonata species resulting in a dynamic species composition

through migration of species to and from the changing sites. Odonata are most abundant from November to January, at the start of and early in the wet season, but their numbers decrease later in the season after the rivers begin to flood since few species can survive in fast flowing water. Their numbers decline again in the cool dry season from July to August (Pinhey 1951). This pattern differs in eurytopic and widespread species, which generally occur throughout the year.

9.4.1 Importance of aquatic and riparian vegetation

The cover provided by exposed aquatic macrophytes is the most important environmental factor for most Odonata as it provides nurseries for nymphs and perches for the adults, as well as shade and protection from predators like birds and larger Anisoptera (Samways & Steytler 1996, Stewart & Samways 1998). Consequently, the species diversity is greater at sites with diverse aquatic macrophytes, in contrast to sites without vegetation where the diversity is low, dominated by a few species that favour such conditions. Any change in the aquatic vegetation results in a change in the structure of the Odonata population. The introduction of an exotic weed, *Salvinia molesta*, to Lake Kariba, and *Pistia stratiotes* and *Eichhornia crassipes* to the Sabie, Crocodile and Letaba rivers in South Africa, have led to an increase in the species diversity (Balinsky 1967, Stewart & Samways 1998), but it would be unwise to allow these invasive and detrimental weeds to flourish merely to increase Odonata diversity. In any case the species favouring these weeds were neither rare, localised endemics nor threatened species.

Water temperature is also an important environmental factor as, among other things, it affects egg development (Samways & Steytler 1996). Water temperature and sunlight-versus-shade are interrelated, as a river with a deep riparian strip that shades the water surface will be cooler. The adults prefer specific sunlight-versus-shade regimes. The physiognomy of the vegetation and not its species composition determines the presence or absence of dragonfly species). Only highly eurytopic zygopteran are found in areas without shade along the banks and with very few aquatic macrophytes. It has therefore been suggested that there should be at least a 20 m strip of riparian vegetation between the edge of the water and the edge of any cultivation to maximise Odonata diversity (Samways & Steytler 1996).

9.4.2 Effects of dam construction

Construction of dams will change currents, vegetation and water temperature, which in turn will affect the dragonfly population. The diversity of Odonata in natural habitats is far richer and less uniform than that of artificial bodies of water where it is poorer and more restricted (Balinsky 1967). The species composition also changes with the rarer, localised species being replaced by common, widespread species. The management of impoundments should aim to create and maintain a large variety of biotopes, with a suitable range of plant architectures and occasional small areas of bare ground if the Odonata diversity is to be maintained. Dams and reservoirs with aquatic macrophytes can be important refugia for species not occurring locally, thus providing an important recolonisation source, particularly after disasters such as heavy flooding or periodic high silt load (Stewart & Samways 1998).

9.4.3 Other effects on Odonata populations

Droughts, as well as disturbances such as water extraction and the removal of riverine and wetland vegetation are the main causes of species loss (Stewart & Samways 1998). Fluctuations in flow rate and high silt loads cause the destruction of river bank vegetation leaving exposed dry sandbanks reducing species diversity. The growth of exotic trees on the banks can also shade out natural bushes

and reeds which are the preferred ovipositing sites of many species. Natural disturbances such as animals trampling and grazing the vegetation and churning the water tend to cause a temporary local reduction in the species diversity (Stewart & Samways 1998), but the continuous presence of cattle could pose a more serious threat. Pollutants such as sewage effluent and fertilizer runoff will make aquatic environments unsuitable for many Odonata species.

There is strong evidence that differences in Odonata assemblages along rivers indicate particular types of human disturbance (Samways & Steytler 1996, Stewart & Samways 1998) and may be useful indicators for river management. Environmental conditions are generally characterized by the proportion of eurytopic species (wide biotope tolerance) to stenotopic species (narrow biotope tolerance), by the number of Anisoptera to Zygoptera species, and also simply in terms of which species are present or not. A highly disturbed river has fewer stenotopic to eurytopic species and proportionally more Anisoptera species, as well as a low species richness (Stewart & Samways 1998). A reference for water management could be obtained by making further collections in the Zambezi Basin, which could then be used to assess changing environmental conditions in future.

9.5 AREAS OF HIGH SPECIES RICHNESS

The deserts and arid parts of central Africa are obviously unfavourable for Odonata. Only those species capable of widespread dispersal because of their ability to fly strongly (like many anisopterans) can populate the waters in such areas. Endemic species are absent (Brinck 1955). On the other hand, in areas of higher rainfall and permanent water there is a richer fauna containing many endemics. The Zambezi River is one of the few rivers of the region that does not dry up or split into muddy pools during years of extreme drought and will therefore always have Odonata along its banks.

The areas that are richest in number of species and genera, but not necessarily in numbers of individuals, are swampy areas along forested tropical streams, which also have a number of endemics. The total number of species from these areas in Africa exceeds 250 (Pinhey 1978) and the upper Zambezi in the Mwinilunga District is one such area with twelve endemics being recorded (*Crocothemis brevistigma*, *Prodasineura flavifacies*, *Aciagrion nodosum*, *Ischnuragrion nodosum*, *Diastatomma selysi*, *Onychogomphus kitchingmani*, *O. quirikii*, *Anax mouri*, *Allorhizucha longistipes*, *Nesciothemis fitzgeraldi*, *Trithemis bifida*, *T. anomala*). Another area rich in Odonata is the Okavango Delta with seven endemics (*Agriocnemis ruberrina*, *Enallagma angolicum*, *Pseudagrion deningi*, *Anax bangweuluensis*, *Trithemis aequais*, *Macromia paludosa*, *Phyllogomphus brunneus*). There are similarities between the populations in the Zambian/Angolan streams and swamps, and the swamps of the Okavango Delta although individual populations are variable, being most dense in quiet pools well stocked with standing and floating vegetation. The reason for the marked similarity between palustrines of Zambia and those of the Okavango Delta is not clearly understood (Pinhey 1978). In the later Tertiary period there is believed to have been a large western drainage basin, and it is also believed that the Upper Zambezi was not connected to its middle and lower reaches but followed a fault line across the Caprivi at or near the Kwando River, which flowed southwards to join the Limpopo.

Species associated with the east coastal lowland forests and bush between Natal and East Africa are also found in the main river valleys, especially along the middle and lower Zambezi River, and in the lowland forests of Malawi (Pinhey 1978). There are eight endemics found in these areas.

Most of the collecting along the Zambezi wetlands has been in the Mwinilunga District in northwestern Zambia and along the Okavango. The large number of species and endemics (see Table 9.1) found in these wetlands in comparison to other areas is more likely to reflect the collecting effort rather than an absence of Odonata. As no collecting has been done in recent years it is not possible to state if any of the species listed below are still present in the area. It is assumed that the collecting that has taken place was done with a sweep net and no quantitative data are available. The larval biotopes are also not known and it is not possible to determine which species, if any, are threatened and should be awarded special conservation status. The species that have been collected from the Middle Zambezi, Lower Shire (Mpatamanga Gorge) and the Zambezi Delta are all widespread ones.

9.6 GAPS IN KNOWLEDGE AND FUTURE RESEARCH

Very little is known about the ecology and habitats of the Odonata of the Zambezi Basin. No collecting has taken place for over 20 years except for two recent trips to Barotseland and the Zambezi Delta, which collected mainly widespread and common species from pools and marshes. No sampling to determine population status has been done, so the present status of all species is not known. Mwinilunga (148 species) and the Okavango (84 species) are the best collected areas. The Odonata of the Barotse floodplain (33 species), Lower Shire (Mpatamanga Gorge) (32 species) and the Zambezi Delta (31 species) are very poorly known, and species collected so far from these areas have all been widespread ones (Table 9.1). As the Zygoptera are more localised and are more affected by environmental conditions than the Anisoptera, any future collecting and monitoring work should concentrate on them. For monitoring purposes there is also a need to standardize collecting techniques such as the catch-per-unit-effort method (Clark & Samways 1996).

9.7 REFERENCES

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- Stewart, D.A.B. & Samways, M.J. (1998). Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African Savanna Game Reserve. *Conservation Biology* **12**(3): 683-692.
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[Back to Contents](#)**Table 9.1** Distribution of Odonata in the Zambezi Basin with particular emphasis on the wetlands. Data are collated from the checklist below and additional collections

(Mwi=Mwinilunga, Bar=Barotse floodplain, Okav=Okavango & Chobe swamps, Kat-VF=Katombora to Victoria Falls. L.Shire = Lower Shire, Mpatamanga Gorge). Localised refers to limited distribution as used by Pinhey.

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
ZYGOPTERA									
Lestidae									
<i>Lestes amicus</i>	X			X				X	
<i>Lestes dissimulans</i>			X	X					X
<i>Lestes ochraceus</i>	X				X				X
<i>Lestes pallidus</i>			X	X					X
<i>Lestes pinheyi</i>	X		X	X					X
<i>Lestes tridens</i>	X							X	
<i>Lestes uncifer</i>	X			X			X		X
<i>Lestes virgatus</i>	X				X				X
Protoneuridae									
<i>Chlorocnemis marshalli</i>		X							X
<i>Chlorocnemis wittei</i>	X							X	
<i>Elatoneura glauca</i>	X		X		X	X			X
<i>Elatoneura tropicalis</i>	X			X					X
<i>Mesocnemis singularis</i>				X		X			X
<i>Prodasineura flavifacies</i>	X							X	
Coenagrionidae									
<i>Aciagrion africanum</i>	X								X
<i>Aciagrion gracile</i>	X				X		X		X
<i>Aciagrion congoense</i>							X	X	
<i>Aciagrion heterosticta</i>				X				X	
<i>Aciagrion macrootithenae</i>	X							X	
<i>Aciagrion nodosum</i>	X							X	
<i>Aciagrion steeleae</i>	X		X					X	
<i>Aciagrion zambiense</i>	X							X	
<i>Agriocnemis angolensis</i>	X			X				X	
<i>Agriocnemis exilis</i>	X	X	X	X		X	X		X
<i>Agriocnemis forcipata</i>	X								X
<i>Agriocnemis gratiosa</i>			X	X					X
<i>Agriocnemis pinheyi</i>	X						X		X
<i>Agriocnemis ruberrina</i>			X					X	
<i>Agriocnemis victoria</i>	X	X	X						X

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
<i>Ceriagrion bakeri</i>	X							X	
<i>Ceriagrion bidentatum</i>	X		X					X	
<i>Ceriagrion glabrum</i>	X	X	X	X	X		X		X
<i>Ceriagrion katamborae</i>			X	X				X	
<i>Ceriagrion kordofanicum</i>	X						X		X
<i>Ceriagrion platystigma</i>	X								X
<i>Ceriagrion sakeji</i>	X		X					X	
<i>Ceriagrion sanguinostigma</i>	X							X	
<i>Ceriagrion suave</i>	X		X	X	X				X
<i>Ceriagrion whellani</i>	X	X							X
<i>Enallagma angolicum</i>			X					X	
<i>Enallagma glaucum</i>		X							X
<i>Enallagma simuatum</i>	X								X
<i>Enallagma subtile</i>				X	X				X
<i>Ischnura senegalensis</i>			X	X	X		X		X
<i>Ischnuragrion nodosum</i>	X							X	
<i>Pseudagrion acaciae</i>			X	X	X	X	X		X
<i>Pseudagrion assegaii</i>			X	X				X	
<i>Pseudagrion chongwe</i>	X							X	
<i>Pseudagrion coelestis</i>		X	X	X			X		X
<i>Pseudagrion commoniae</i>			X	X	X		X		X
<i>Pseudagrion deningi</i>			X					X	
<i>Pseudagrion fisheri</i>	X		X					X	
<i>Pseudagrion gamblesi</i>	X								X
<i>Pseudagrion glaucescens</i>	X		X	X					X
<i>Pseudagrion greeni</i>	X							X	
<i>Pseudagrion hageni</i>	X								X
<i>Pseudagrion hamoni</i>	X		X	X	X	X	X		X
<i>Pseudagrion helenae</i>			X			X	X	X	
<i>Pseudagrion kersteni</i>	X				X	X			X
<i>Pseudagrion kibalense</i>	X							X	
<i>Pseudagrion makabusiensis</i>	X							X	
<i>Pseudagrion massaicum</i>			X		X	X			X
<i>Pseudagrion melanicterum</i>	X								X
<i>Pseudagrion nubicum</i>				X	X				X
<i>Pseudagrion rufostigma</i>	X		X	X				X	
<i>Pseudagrion salisburyense</i>	X			X					X
<i>Pseudagrion sjöstedti</i>	X		X	X					X
<i>Pseudagrion spernatum</i>	X			X					X

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
<i>Pseudagrion sublacteum</i>	X		X	X	X	X			X
<i>Pseudagrion sudanicum</i>			X	X	X				X
<i>Pseudagrion williamsi</i>	X							X	
Chlorocyphidae									
<i>Chlorocypha frigida</i>	X							X	
<i>Chlorocypha luminosa</i>	X								X
<i>Chlorocypha wittei</i>	X							X	
<i>Platycypha caligata</i>	X			X	X				X
Calopterygidae									
<i>Phaon iridipennis</i>	X		X	X	X	X			X
<i>Umma distincta</i>	X							X	
Total Zygoptera (77)	55	7	31	31	18	10	13	31	45
ANISOPTERA									
Gomphidae									
<i>Cinitogomphus dundoensis</i>			X					X	
<i>Crenigomphus cornutus</i>	X			X				X	
<i>Crenigomphus hartmanni</i>	X			X		X			X
<i>Diastatomma selysi</i>	X							X	
<i>Gomphidia quarrei</i>			X	X					X
<i>Ictinogomphus ferox</i>		X	X	X					X
<i>Lestinogomphus angustus</i>			X	X					X
<i>Neurogomphus uelensis</i>							X		
<i>Neurogomphus wittei</i>				X				X	
<i>Notogomphus praetorius</i>	X								X
<i>Onychogomphus kitchingmani</i>	X							X	
<i>Onychogomphus quirikii</i>	X							X	
<i>Paragomphus cataractae</i>				X				X	
<i>Paragomphus cognatus</i>	X								X
<i>Paragomphus elpidius</i>			X	X	X				X
<i>Paragomphus genei</i>			X	X	X		X		X
<i>Paragomphus nyassicus</i>				X				X	
<i>Paragomphus sabicus</i>				X	X				X
<i>Paragomphus zambeziensis</i>				X	X			X	
<i>Phyllogomphus brunneus</i>			X	X				X	
Aeshnidae									
<i>Acanthagyma sextans</i>	X								X
<i>Aeshna wittei</i>	X							X	
<i>Anax bangweuluensis</i>			X					X	

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
<i>Crocothemis divisa</i>	X								X
<i>Crocothemis erythraea</i>		X					X		X
<i>Crocothemis sanguinolenta</i>	X		X	X	X	X			X
<i>Crocothemis saxicolor</i>	X				X			X	
<i>Diplacodes deminuta</i>		X						X	
<i>Diplacodes lefebvrei</i>	X	X	X	X	X		X		X
<i>Diplacodes okavangoensis</i>	X	X	X					X	
<i>Eleuthemis buettikoferi</i>	X			X					X
<i>Hadrothemis camerensis</i>	X								X
<i>Hadrothemis defecta</i>	X								X
<i>Hadrothemis scabrifrons</i>	X						X		X
<i>Hadrothemis versuta</i>	X								X
<i>Hemistigma albipuncta</i>	X	X	X	X	X		X		X
<i>Monardithemis flava</i>	X							X	
<i>Nesciothemis farinosum</i>			X		X				X
<i>Nesciothemis fitzgeraldi</i>	X							X	
<i>Notiothemis robertsi</i>	X								X
<i>Olpogastra fuelleborni</i>				X	X	X			X
<i>Olpogastra lugubris</i>		X	X	X		X			X
<i>Orthetrum abbotti</i>	X			X	X				X
<i>Orthetrum angustiventre</i>	X								X
<i>Orthetrum austeni</i>	X								X
<i>Orthetrum brachiale</i>	X	X	X	X		X	X		X
<i>Orthetrum chrysostigma</i>		X	X	X	X	X	X		X
<i>Orthetrum guineese</i>	X								X
<i>Orthetrum hintzi</i>	X								X
<i>Orthetrum icteromelas</i>	X	X	X	X					X
<i>Orthetrum julia</i>	X						X		X
<i>Orthetrum machadoi</i>	X		X						X
<i>Orthetrum macrostigma</i>	X							X	
<i>Orthetrum microstigma</i>	X								X
<i>Orthetrum monardi</i>	X								X
<i>Orthetrum robustum</i>	X		X					X	
<i>Orthetrum saegeri</i>	X							X	
<i>Orthetrum stemmale</i>							X		
<i>Orthetrum trinacrium</i>	X	X	X		X		X		X
<i>Palpopleura jucunda</i>	X				X				X
<i>Palpopleura lucia</i>	X	X		X			X		X
<i>Pantala flavescens</i>			X	X	X	X			X

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
<i>Zygonyx natalensis</i>	X			X		X			X
<i>Zygonyx torridus</i>	X		X		X	X			X
Total Anisoptera (140)	93	26	53	57	34	22	23	44	94
TOTAL SPECIES (217)	148	33	84	88	52	32	36	75	139

9.8 CHECKLIST AND ECOLOGICAL NOTES

The following checklist has been compiled from:

- specimens in the Natural History Museum, Bulawayo.
- Pinhey, E. (1962). A descriptive catalogue of the Odonata of the African Continent (up to December 1959) Part 1-2. *Publicações Culturais da Companhia de Diamantes de Angola* **59**: 1-322.
- Additional references listed below.

ZYGOPTERA

LESTIDAE (21)

Lestes amicus *Martin, 1910*

Very local and gregarious, preferring wet patches in forest or swamp-forest.

Distribution: Zimbabwe, Mozambique, Angola, S Tanzania.

Lestes dissimulans *Fraser, 1955*

Found in swamps and grassy pools, quiet streams, sometimes temporary rain pools

Distribution: Widespread; S Mozambique, Transvaal, Zimbabwe, Botswana, Zaire, Angola, Tanzania, Kenya, Uganda, DRC, Gabon, Chad, Nigeria, Senegal.

Lestes ochraceus *Selys, 1862*

Usually found at stagnant reedy or grassy pools or quiet streams.

Distribution: Zimbabwe, Malawi, Zambia, DRC, Tanzania, Kenya, Uganda, S Sudan, Cameroon, Nigeria, Burkino Faso.

Lestes pallidus *Rambur, 1842*

Common and widespread species found in open country, favouring grassy or reedy pools and streams, or at times the bush, grass or low vegetation at some distance from water. Also occurs at grass-fringed pools in arid sandy waste lands.

Distribution: Throughout Afrotropics, except in forests.

Lestes pinheyi *Fraser, 1955*

Found at reedy or grassy pools; most commonly in palustrine swampy conditions.

Distribution: Zimbabwe, Zambia, E Angola, DRC, Nigeria.

Lestes tridens *McLachlan, 1895*

Very local in open reed beds or at reedy, grassy margins of small or large pools, even lakes.

Distribution: Natal, Transvaal, Mozambique, Zimbabwe, Zambia, E Angola, Zaire, Tanzania, Kenya, Uganda, Somalia, Nigeria.

Lestes uncifer *Karsch, 1899*

A rather uncommon species, found near reedy pools or streams but generally amongst bush or clumps of tress nearby.

Distribution: Natal, Mozambique, Zimbabwe, Zambia, DRC, Tanzania, Uganda, Somalia, Nigeria.

Lestes virgatus (*Burmeister, 1839*)

Locally common and widespread species found in woodland or forest, sometimes in thick bush. Favours small pools, or sluggish forest streams.

Distribution: E Cape northwards, inland & coastal to Ethiopia, equatorial, C & W Africa.

PROTONEURIDAE**Chlorocnemis marshalli** *Ris, 1921* (10)

Found in heavy forest, sometimes montane forest, but quite often in thick patches of bush.

Distribution: Zimbabwe, Zambia, Malawi, Mozambique.

Chlorocnemis wittei *Fraser, 1955* (10)

Distribution: Zambia, DRC.

Elattoneura glauca (*Selys, 1860*) (8,18)

Locally common and gregarious on banks of streams, particularly in shade of trees

Distribution: Widespread throughout the Afrotropics.

Elattoneura tropicalis *Pinhey, 1974* (5,15,18)

On banks of well shaded streams and rivers.

Distribution: Zambia, Malawi, DRC, Uganda.

Mesocnemis singularis (*Karsch, 1891*) (8,18,22)

Frequents fast waters of rivers and streams; appears to be gregarious.

Distribution: Widely distributed in Afrotropics.

Prodasineura flavifacies *Pinhey, 1981* (24)

Only known from Ikelenge (Mwinilunga).

COENAGRIONIDAE**Aciagrion africanum** *Martin, 1908*

Prefers swamps or swampy verges of streams.

Distribution: Zimbabwe northwards to DRC.

Aciagrion congoense (*Sjöstedt, 1917*)

Slow streams or reedy and grassy pools.

Distribution: Malawi, Tanzania, Uganda, Mozambique, Zambia

Aciagrion gracile (*Sjöstedt, 1909*)

Found at quite reedy or grassy pools, streams and swamps.

Distribution: Malawi, Tanzania, Uganda, Mozambique, Zambia, Zimbabwe.

Aciagrion heterosticta *Fraser, 1955*

Found in swamps or swampy pools verging on slow streams.

Distribution: Uganda, DRC, Zambia.

Aciagrion macrootithenae *Pinhey, 1972*

Found in swamps and eggs possibly laid through mud or through submerged plants into mud.

Distribution: Angola, DRC, Upper Zambezi.

Aciagrion nodosum (*Pinhey, 1964*)

Found in swampy gallery forest streams.

Distribution: Only in Mwinilunga area.

Aciagrion steeleae *Kimmins, 1955* (18)

Found in swamps or the swampy margins of streams, pools and lakes.

Distribution: Zambia, Angola, Botswana.

Aciagrion zambiense *Pinhey, 1972*

Found in swamps near or in gallery forest.

Distribution: Zambia, E Angola.

Agriocnemis angolensis *Longfield, 1945* (18)

Distribution: Angola, Namibia.

Agriocnemis angolensis spatulae *Pinhey, 1974* (8,18)

Only known from Ikelenge Swamp, Mwinilunga.

Agriocnemis exilis *Selys, 1869*

Distribution: Nigeria, Uganda, Tanzania, Malawi, Zambia, Mozambique, Zimbabwe, Botswana, DRC, Angola.

Agriocnemis forcipata *Le Roi, 1915*

Distribution: Sudan, Cameroon; Central African Republic, Uganda, DRC, Zambia.

Agriocnemis gratiosa *Gerstaecker, 1891* (18)

Distribution: Sudan, Tanzania, Uganda, Malawi, Zambia, Mozambique, Botswana, Natal.

Agriocnemis pinheyi *Balinsky, 1951*

Distribution: Zambia, Zimbabwe, Mozambique, Natal.

Agriocnemis ruberrina *Balinsky, 1961* (18)

Only known from Natal and Okavango Swamps.

Agriocnemis victoria *Fraser, 1928* (18)

Distribution: Sierra Leone, Nigeria, Cameroon, Central African Republic, Uganda, DRC, Angola, Zambia, Botswana.

Ceriagrion bakeri *Fraser, 1951* (3)

Distribution: Uganda, Nigeria, Upper Zambezi.

Ceriagrion bidentatum *Fraser 1941* (3, 18)

Local in forests of Central and tropical Africa.

Distribution: Uganda, Angola, Zambia, DRC, Nigeria, Zambezi Basin.

Ceriagrion glabrum (*Burmeister, 1839*) (18)

A common species in streams and pools well supplied with reeds.

Distribution: Widely distributed over the Afrotropics and parts of Arabia.

Ceriagrion katamborae *Pinhey, 1961* (2,9,18)

Found in swampy streams.

Distribution: Upper Zambezi.

Ceriagrion kordofanicum *Ris, 1924*

Distribution: Sudan, Kenya, Uganda, Upper Zambezi.

Ceriagrion platystigma *Fraser, 1941* (3)

Distribution: Uganda, Cameroon, DRC, Zambia, S Nigeria, Upper Zambezi.

Ceriagrion sakeji *Pinhey, 1963*

Found in swampy streams.

Distribution: Upper Zambezi.

Ceriagrion sanguinostigma *Fraser, 1955*

Distribution: DRC, Upper Zambezi.

Ceriagrion suave *Ris, 1921* (3,18)

Distribution: Fairly widespread; almost abundant in some localities. Zimbabwe, DRC, Angola, Kenya, Nigeria, Botswana, Zambia.

Ceriagrion whellani *Longfield, 1952* (3)

Fairly localised species.

Distribution: Zimbabwe, Zambia, DRC, Lake Victoria, Sierra Leone.

Enallagma angolicum *Pinhey, 1966* (18)

Distribution: Zambia, Botswana, Angola.

Enallagma sinuatum *Ris, 1921*

Apparently rather scarce.

Distribution: DRC, Natal, Zimbabwe, Zambia, S Tanzania.

Enallagma subtile *Ris, 1921* (18)

Occurs on rivers and streams.

Distribution: South Africa, DRC, Tanzania, Kenya, Zimbabwe, N Nigeria.

Ischnuragrion nodosum *Pinhey, 1964* (5)

Known only from the Ikelenge area, Mwinilunga.

Ischnura senegalensis (*Rambur, 1842*) (9 18)

Widespread in most freshwater habitats and has a very high tolerance of ecological conditions.

Distribution: Throughout the African continent and Asia.

Pseudagrion acaciae *Förster, 1906* (8,18)

Distribution: Widespread in Africa.

Pseudagrion assegaii *Pinhey, 1950* (18)

Very local species.

Distribution: Transvaal, Botswana, Zimbabwe, Zambia, S DRC.

Pseudagrion chongwe *Pinhey, 1961*

Distribution: Angola, N Zambia.

Pseudagrion coelestis *Longfield, 1945* (18)

Fairly localised species.

Distribution: Angola, Botswana, Zimbabwe, Zambia.

Pseudagrion commoniae *Förster, 1902* (18)

Distribution: Zimbabwe, N Botswana, Mozambique northwards to Kenya.

Pseudagrion deningi *Pinhey, 1961* (18)

Distribution: Bangweulu & Okavango Swamps.

Pseudagrion fisheri *Pinhey, 1961* (18)

Distribution: Angola, Zambia.

Pseudagrion gamblesi *Pinhey, 1978* (19)

Large species found at fast flowing waters, often near cascades or rapids where the streams or rivers are open, with grasses and sedges on the banks.

Distribution: Natal, Transvaal, Zimbabwe, Mozambique, Zambia, Kenya.

Pseudagrion glaucescens *Selys, 1876* (18)

Favours streams and rivers rather than pools.

Distribution: Mozambique, Zambia, Botswana, Zimbabwe, Kenya.

Pseudagrion greeni *Pinhey, 1961*

Distribution: Zambia.

Pseudagrion hageni *Karsch, 1893* (18)

Distribution: Nearly all tropical and subtropical Africa.

Pseudagrion hamoni *Fraser, 1955* (8)

Prefers rivers or streams with adequate fringe vegetation and shade.

Distribution: Zimbabwe, Mozambique northwards to Kenya, DRC, Uganda, Nigeria, S Sudan.

Pseudagrion helenae *Balinsky, 1964* (1,18)

Distribution: Zambia, Botswana, Malawi.

Pseudagrion kersteni (*Gerstaecker, 1869*) (8)

One of the commonest Zygoptera. Frequents streams or pools but not swamps.

Distribution: Most of Afrotropics.

Pseudagrion kibalense *Longfield, 1959*

Distribution: Localised species; Uganda, DRC, Zambia.

Pseudagrion makabusiensis *Pinhey, 1950*

Found very locally on rushes or grasses in very sluggish parts of streams.

Distribution: Zambia, Zimbabwe.

Pseudagrion massaicum *Sjöstedt, 1909* (8,18)

Locally common over streams, pools or even broad rivers, flying strongly and low over the water; settling on leaves of water lily etc. Rather swift for a Coenagriid.

Distribution: Cape northwards to Kenya, Uganda, DRC, Angola.

Pseudagrion melanicterum *Selys, 1876*

Distribution: Zambia, DRC, Uganda, Cameroon, Nigeria, W Africa.

Pseudagrion nubicum *Selys, 1876* (18)

Locally common and gregarious in summer over stagnant pools.

Distribution: Zimbabwe to Sudan and W Africa.

Pseudagrion rufostigma *Longfield, 1945* (18)

Favours swamps rather than streams or rivers.

Distribution: Angola, Zambia, Botswana, Zimbabwe.

Pseudagrion salisburyense *Ris, 1921* (18)

Common and gregarious along grassy banks of streams and pools throughout the year.

Distribution: southern & eastern Africa.

Pseudagrion sjöstedti *Förster, 1906* (18)

Found along rivers and streams, sometimes over pools and swamps.

Distribution: subtropical & tropical Africa.

Pseudagrion spernatum *Selys, 1881*

Distribution: South Africa, Mozambique, Zimbabwe, Zambia.

Pseudagrion sublacteum (*Karsch, 1893*) (8,18)

Somewhat local species found flying over rather fast-flowing rivers or broad streams, not over still pools, and sometimes at edges of rapids. Has rather a strong flight for a Coenagriid.

Distribution: South Africa, Botswana, Zimbabwe, Mozambique, Kenya, Uganda, Nigeria.

Pseudagrion sudanicum *Le Roy, 1915* (18)

Distribution: Zimbabwe, Uganda, Botswana.

Pseudagrion williamsi *Pinhey, 1964* (7)

Distribution: Angola, N Zambia.

CHLOROCYPHIDAE**Chlorocypha frigida** *Pinhey, 1961* (2)

A shy dragonfly, appearing in sunlit spots at forested streams and waterfalls.

Distribution: Upper Zambezi.

Chlorocypha luminosa (*Karsch, 1893*) (3)

Distribution: Widespread & common; Tanzania, Malawi, Zimbabwe, Mozambique, Zambia, Ghana, Nigeria.

Chlorocypha wittei (*Fraser, 1955*) (18)

Distribution: DRC, Angola, Zambia.

Platycypha caligata (*Selys, 1853*) (18)

Common on streams or rivers; not a swamp species.

Distribution: Tanzania, Somalia, DRC, Mozambique, Zambia, Zimbabwe, Namibia, Angola.

CALOPTERYGIDAE

Phaon iridipennis (*Burmeister, 1839*) (18)

Locally common on shaded streams and pools in forest or even clumps of bush.

Distribution: All tropical and subtropical Africa.

Umma distincta *Longfield, 1933* (11)

Distribution: DRC, Zambia, Angola.

ANISOPTERA

GOMPHIDAE

Cinogomphus dundoensis (*Pinhey, 1961*) (18,9)

Found in swampy areas.

Distribution: Angola, Zambia, Botswana.

Crenigomphus cornutus *Pinhey 1956* (18)

Favours long grass near the margins of fast flowing rivers and streams.

Distribution: Upper Zambezi.

Crenigomphus hartmanni (*Förster, 1898*) (8)

Found over pools and streams, settling on low vegetation.

Distribution: From South Africa to Tanzania, DRC, Angola.

Diastomma selysi *Schouteden, 1934*

Distribution: Upper Zambezi.

Gomphidia quarrei (*Schouteden, 1934*) (18)

Locally common near wooded fringe of rivers.

Distribution: DRC, Uganda, Angola, Botswana, Zimbabwe.

Ictinogomphus ferox (*Rambur, 1842*) (18)

Common, found on reedy pools or rivers.

Distribution: Natal to East, Central and tropical W Africa.

Lestinogomphus angustus *Martin, 1912* (18)

Favours the wooded fringes or fast flowing rivers.

Distribution: Kenya, Uganda, DRC, Zambia, Botswana, Zimbabwe.

Neurogomphus uelensis (*Schouteden, 1934*)

Neurogomphus wittei *Schouteden, 1934* (5)

Only found in grasslands at Katombora Rapids.

Notogomphus praetorius (*Selys, 1878*)

Found on banks of reedy streams, rivers and pools.

Distribution: South Africa, Zimbabwe, Zambia, Angola, DRC.

Onychogomphus kitchingmani *Pinhey, 1960*

Only known from Mwinilunga area.

Onychogomphus quirikii *Pinhey, 1964* (5)

Only known from Mwinilunga area.

Paragomphus cataractae *Pinhey, 1963*

Only known from Katombora.

Paragomphus cognatus (*Rambur, 1842*)

Common species in open, rocky streams.

Distribution: From Cape Province to Ethiopia, and from Kenya westwards to Nigeria.

Paragomphus elpidius (*Ris, 1921*) (18)

Found near river margins, sparingly in swamps.

Distribution: Natal, along Zambezi River, Malawi, DRC, Kenya, Uganda.

Paragomphus genei (*Selys, 1841*) (18)

Found near rivers, streams and pools. Commonest and most widespread of the African Gomphidae.

Distribution: From South Africa to S Europe.

Paragomphus nyassicus *Kimmins, 1955*

Distribution: Malawi, Zimbabwe.

Paragomphus sabicus *Pinhey, 1950* (18)

Found on well flowing rivers and streams.

Distribution: Sabi Valley to Zambia, Mozambique.

Paragomphus zambeziensis *Pinhey, 1960*

Only known from Upper and Middle Zambezi.

Phyllogomphus brunneus *Pinhey, 1976* (18)

Only known from Upper Zambezi.

AESHNIDAE**Acanthagyma sextans** (*McLachlan, 1895*) (3)

Distribution: West Africa, Angola, Zambia.

Aeshna wittei *Fraser, 1955* (23)

Distribution: DRC, Zambia.

Anax bangweuluensis *Kimmins, 1955* (18)

Distribution: Zambia, Botswana.

Anax congoliath *Fraser, 1953* (3)

Distribution: DRC, Zambia.

Anax imperator *Leach, 1815* (18)

Distribution: recorded from nearly all of the Afrotropical Region, except at higher altitudes.

Anax mouri *Pinhey, 1981* (23)

Only known from Mwinilunga area.

Anax speratus *Hagen, 1867* (8,18)

Tends to favour rivers or streams more than pools.

Distribution: Most of continental Afrotropics.

Anax tristis *Hagen, 1867* (18)

Widespread and powerful flier, often seen over pools rather than rivers and streams.

Distribution: Zimbabwe to Kenya, Uganda, Namibia, Central & W Africa and neighbouring islands.

Gynacantha sevastopuloi (*Pinhey, 1961*) (2)

Distribution: Uganda, Malawi, Zambia.

Gynacantha vesiculata *Karsch, 1891*

Distribution: Afrotropics.

Gynacantha villosa *Gruenberg, 1902* (18)

Distribution: Mozambique, Malawi, Zambia, Botswana, Tanzania, Uganda, DRC, Nigeria.

Heliaeschna cynthiae *Fraser, 1939* (3)

Distribution: Angola, NW Zambia.

Heliaeschna trinervulata *Fraser, 1955*

Distribution: Angola, DRC, Upper Zambezi.

Hemianax ephippiger (*Burmeister, 1839*) (18)

Distribution: Common migrant found over nearly all of Africa and neighbouring islands.

CORDULIIDAE

Macromia bifasciata (*Martin, 1912*) (18)

Harks up and down in forest or thick bush, near streams or over rivers and lakes.

Distribution: W Africa, DRC, Zambia, Botswana, Zimbabwe.

Macromia bispina *Fraser, 1954*

Distribution: Uganda, Upper Zambezi.

Macromia congolica *Fraser, 1955*

Distribution: DRC, Zimbabwe.

Macromia kimminsi *Fraser, 1954* (18)

Distribution: Kenya, Uganda, Botswana, Zambia.

Macromia overlaeti *Schouteden, 1934*

Distribution: DRC, Zambia.

Macromia paludosa *Pinhey, 1976* (18)

Only known from S Zambia and N Botswana.

Macromia picta *Selys, 1871* (8,18)

Common in bush country harking up and down, occasionally gregarious.

Distribution: South Africa, Zimbabwe, Malawi, Botswana, Zambia, Tanzania, Kenya, Uganda, DRC, Angola, Nigeria.

Macromia unifasciata *Fraser, 1954*

Distribution: DRC, Zambia.

LIBELLULIDAE

Acisoma panorpoides *Rambur, 1842* (18,25)

Found on quiet rivers or streams, pools or swamps.

Distribution: Africa and Oriental Regions.

Acisoma trifoldum *Kirby, 1889*

Distribution: Kenya, Uganda, DRC, Zambia, Angola, Cameroon, W Africa.

Aethiothemis bequaerti *Ris, 1919*

Distribution: DRC, Zambia.

Aethiothemis diamangae *Longfield, 1959* (3)

Distribution: Angola, Zambia.

Aethiothemis discrepans *Lieftinck, 1969* (18)

Found in reedy or grassy pools.

Distribution: DRC, Zambia, Botswana, Malawi, Central Africa to Nigeria.

Aethiothemis mediofasciata *Ris, 1931*

Distribution: Angola, Zambia.

Aethriamanta rezia *Kirby, 1889* (18)

Settles on reeds or twigs over or near water. Not a common species.

Distribution: Mozambique, Botswana, Zambia, DRC, Tanzania, Kenya, Uganda, W Africa.

Allorhizucha klingi *Karsch, 1890*

Found in dense forest.

Distribution: DRC, Angola, Zambia, Cameroon, W Africa.

Allorhizucha longistipes *Pinhey, 1964* (5)

Only known from Mwinilunga area.

Allorhizucha preussi *Karsch, 1891*

Distribution: Uganda, DRC, Zambia, Cameroon.

Archaeophlebia victoriae *Pinhey, 1963*

Only known from Victoria Falls.

Atoconeura biordinata *Karsch, 1899*

Found in thick bush or forest fringing streams and rivers.

Distribution: Afrotropical region.

Brachythemis lacustris (*Kirby, 1889*) (8)

Locally gregarious in swampy conditions.

Distribution: In suitable swampy areas throughout tropical and subtropical Africa.

Brachythemis leucosticta (*Burmeister, 1839*) (18,8)

Found over cleared banks of any pool or even near a temporary puddle.

Distribution: Throughout most of the African Continent, S Europe and W Asia.

Brachythemis wilsoni *Pinhey, 1952* (18)

Distribution: Sudan, Nigeria, Uganda, Botswana.

Bradinopyga cornuta *Ris, 1911* (18,8)

Favours rocks near faster running streams or rivers.

Distribution: South Africa, Mozambique, Malawi, Zimbabwe, Tanzania, Kenya, Zambia.

Chalcostephia flavifrons *Kirby, 1889* (18)

Prefers reedy or grassy pools and swamps to rivers and streams.

Distribution: Most of Afrotropical region.

Crocothemis brevistigma *Pinhey, 1961* (2,3)

Only known from the Mwinilunga area.

Crocothemis divisa *Baumann, 1898*

Found over streams in forest or bush, with rocks on which to settle.

Distribution: Zimbabwe, Malawi, Zambia, Tanzania, Kenya, Uganda, DRC, Sudan, Cameroon, W. Africa.

Crocothemis erythraea (*Brullé, 1832*)

Very common throughout southern Africa.

Crocothemis sanguinolenta (*Burmeister, 1839*) (18,8)

Locally found on rocks in open country on rivers, streams, pools and swamps.

Distribution: Throughout continental Afrotropical region.

Crocothemis saxicolor *Ris, 1919* (2,3,8)

Local over or near rocky streams or pools.

Distribution: Zimbabwe, Zambia, Malawi.

Diplacodes deminuta *Lieftinck, 1969*

Localised species of shallow marshes.

Diplacodes lefebvrei (*Rambur, 1842*) (18,8)

Abundant at quieter waterways, pools, swamps, or margins of rivers.

Distribution: Over all continental Africa.

Diplacodes okavangoensis *Pinhey, 1976* (18)

Swamp species found from the Okavango Delta to W Zambia.

Eleuthemis buettikoferi *Ris, 1910*

Distribution: Zambia, Tanzania, Uganda, W Africa.

Enallagma glaucum (*Burmeister, 1839*)

Very common species at ponds throughout southern Africa.

Hadrothemis camerensis (*Kirby, 1889*)

Distribution: DRC, Uganda, Cameroon, W Africa, Angola, Zambia.

Hadrothemis defecta (*Karsch, 1891*)

Distribution: DRC, Cameroon, Angola, W Africa, Mozambique, Zambia, Zimbabwe.

Hadrothemis scabrifrons *Ris, 1909*

Distribution: Tanzania, Kenya, DRC, Cameroon, Zambia.

Hadrothemis versuta (*Karsch, 1891*)

Distribution: W Africa, DRC, Zambia.

Hemistigma albipuncta (*Rambur, 1842*) (18)

Common and widespread in open swamp, reedy pools in bush, woodland or forest.

Distribution: Over most of continental Afrotropics.

Monardithemis flava *Longfield, 1945*

Distribution: Angola, Zambia.

Nesciothemis farinosum (*Förster, 1898*) (18)

Common species favouring open country, grassland or swamps, in bush or woodland.

Distribution: Over all continental Afrotropics.

Nesciothemis fitzgeraldi *Longfield, 1955*

Distribution: Zambia.

Notiothemis robertsi *Fraser, 1944*

Distribution: Uganda, Nigeria, Cameroon, DRC, Zimbabwe, Zambia.

Olpogastra fuelleborni *Gruenberg, 1902* (18)

Species settles on bushes overhanging the river.

Distribution: South Africa, Zimbabwe, Malawi, Tanzania, Kenya, Sudan, DRC, Angola, Nigeria.

Olpogastra lugubris *Karsch, 1895* (18,8)

Found at reed fringed rivers, streams or large reedy pools.

Distribution: Namibia, Zimbabwe, Botswana, Zambia, Malawi, Tanzania, DRC, Mozambique, Kenya, Uganda, Sudan, W Africa.

Orthetrum abbotti *Calvert, 1892*

Distribution: Most of the Afrotropical region.

Orthetrum angustiventre (*Rambur, 1842*) (3)

Distribution: Angola, W Zambia, N Uganda, S Sudan, N Nigeria, W Africa.

Orthetrum austeni (*Kirby, 1900*)

Distribution: Zambia, DRC, Cameroon, W Africa.

Orthetrum brachiale (*Beauvies, 1805*) (18,8)

Common in bush country, sometimes in forest.

Distribution: Throughout continental Africa.

Orthetrum chrysostigma (*Burmeister, 1839*) (18)

Found in streams, rivers, pools in open country. Highly tolerant of temperature gradients and possibly also pH values.

Distribution: Throughout most of continental Africa; also neighbouring Asia and Europe.

Orthetrum guineese *Ris, 1909*

Found over streams in bush or forest.

Distribution: Natal to Tanzania and Somalia, Angola, Zambia, Nigeria, W Africa.

Orthetrum hintzi *Schmidt, 1951*

Found over streams and pools in bush or forest.

Distribution: Natal to Kenya, Angola, Zambia northwards to Nigeria and W Africa.

Orthetrum icteromelas *Ris, 1909* (18)

Found over warmer streams and pools in bush country.

Distribution: Natal, Mozambique, Tanzania, Angola, Botswana, Zambia, Cameroon, Sudan.

Orthetrum julia *Kirby, 1900*

Distribution: South Africa to Ethiopia, Angola, Zambia, Mozambique, DRC, Nigeria, W Africa.

Orthetrum machadoi *Longfield, 1945* (18)

Common in swamps.

Distribution: Most parts of the Afrotropics.

Orthetrum macrostigma *Longfield, 1945*

Distribution: Angola, Zambia, Tanzania, DRC.

Orthetrum microstigma *Ris, 1911*

Distribution: Angola, Zambia, Cameroon, Uganda, Kenya, W Africa.

Orthetrum monardi *Schmidt, 1951*

Distribution: Zambia, DRC, Kenya, Nigeria, Cameroon.

Orthetrum robustum *Balinsky, 1965* (18)

Favours woodland.

Distribution: Botswana, Zambia.

Orthetrum saegeri *Pinhey, 1966*

Distribution: DRC, Uganda, Cameroon, Zambia.

Orthetrum stemmale stemmale (*Burmeister, 1839*)

Thick bush or forest in warmer areas.

Distribution: Mozambique and Transvaal to equatorial E and W Africa, also Madagascar and Mauritius.

Orthetrum trinacrium (*Selys, 1841*) (18)

Prefers rivers, streams and pools in rather open country.

Distribution: Natal to North Africa, mainly in the E half.

Palpopleura jucunda *Rambur, 1842* (18)

Locally common at grassy pools and swamps.

Distribution: Most of continental Afrotropics.

Palpopleura lucia (*Drury, 1773*) (18,8)

Inhabits pools, swamps and the calmer stretches of streams and rivers.

Distribution: Locally abundant over most of continental Afrotropics.

Pantala flavescens (*Fabricius, 1798*) (18)

Distribution: Throughout Africa and neighbouring islands, Europe, Asia, Australia, Americas.

Parazyxomma flavicans (*Martin, 1908*) (18)

A shy species, only found in the shade of trees.

Distribution: Zimbabwe, Botswana, Malawi, DRC, Uganda.

Philonomon luminans (*Karsch, 1893*)

Prefers reedy pools in warm open country, not common in the central swamps.

Distribution: Natal northwards to Somalia, central and W Africa.

Porpacithemis dubia *Fraser, 1954*

Distribution: DRC, Zambia.

Porpax asperipes *Karsch, 1896*

Distribution: DRC, Angola, Zambia, Cameroon, W Africa.

Porpax risi *Pinhey, 1958* (7)

Very local species found in swamps.

Distribution: Zimbabwe, Mozambique, Zambia, Angola.

Rhyothemis fenestrina (*Rambur, 1842*) (18)

Occurs in great numbers, fluttering on the verge of forests, thick bush or woodland, near swamps.

Distribution: Botswana, northwards to Uganda and west equatorial Africa.

Rhyothemis mariposa *Ris, 1913* (18)

Distribution: Namibia, Zambia, Angola, DRC.

Rhyothemis notata (*Fabricius, 1781*)

Distribution: Botswana, Zambia, DRC, W Africa.

Rhyothemis semihyalina (*Désjardins, 1832*) (18)

Found at reed fringed rivers and streams, grassy or reedy pools and swamps.

Distribution: Continental Africa.

Sympetrum fonscolombi (*Selys, 1837*) (18)

Found in many of the more open, often arid regions.

Distribution: Scattered localities throughout continental Africa.

Sympetrum navasi *Lacroix, 1921* (18)

Common on swampy verges.

Distribution: Uganda, Zambia, Botswana, W Africa.

Tetrathemis polleni (*Selys, 1869*) (8)

Local species on quiet well shaded pools or sluggish streams under shade, at low elevations.

Distribution: Natal to Kenya, DRC, Uganda, Nigeria.

Thermochoria equivocata *Kirby, 1889*

Distribution: Uganda, Zambia, DRC, Cameroon, W Africa.

Tholymis tillarga (*Fabricius, 1798*) (18)

Distribution: Throughout Afrotropics; Asia and Australia.

Tramea basilaris (*Beauvois, 1817*) (= *Trapezostigma basiliare*) (18)

Found flying swiftly over small or large bodies of water in open country or forest clearings.

Distribution: Most of Afrotropics and Asia.

Tramea burmeisteri *Kirby, 1889* (= *Trapezostigma burmeisteri*)

Very common, widespread species.

Trithemis aconita *Lieftinck, 1969* (18)

Found in thick bush fringing rivers and streams.

Distribution: Natal to Kenya coast, Zambezi valley to Mwinilunga, Malawi, DRC, W Africa.

Trithemis aequalis *Lieftinck, 1969* (18)

Settles on reeds or sedges in streams or on low vegetation away from the banks.

Distribution: Zambia, Okavango.

Trithemis annulata *(Beauvois, 1805)* (18,8)

Found on or near rivers, streams and pools; settling frequently on reeds, grasses or rocks.

Distribution: Widely distributed in Africa and Asia.

Trithemis arteriosa *(Burmeister, 1839)* (18,8)

Found over or near most freshwater sources, whether stagnant or fast flowing, throughout the year. Not a swamp species, being found only on the fringes.

Distribution: Widely distributed; the most abundant anisopteran in Africa.

Trithemis anomala *Pinhey, 1956*

Found in open swamps, reedy pools.

Distribution: Only known from NW Zambia.

Trithemis bifida *Pinhey, 1970*

Found in thick gallery forest.

Distribution: Mwinilunga area, Zambia.

Trithemis dichroa *Karsch, 1893*

Small species found in forest or thick bush, quite streams and pools.

Distribution: W Africa, Cameroon, Uganda, DRC, Zambia.

Trithemis donaldsoni *(Calvert, 1899)*

Local, not usually abundant. Generally in bush country, on rivers and streams; sometimes in rather arid places.

Distribution: Natal, Zimbabwe, Malawi, Mozambique northwards to Kenya, Somalia, Ethiopia, DRC, Uganda, Nigeria.

Trithemis dorsalis *(Rambur, 1842)*

On streams and pools in open country.

Distribution: South Africa, Mozambique, Kenya, Zimbabwe, Angola, Zambia, DRC.

Trithemis furva *Karsch, 1899*

On streams, rivers or reed-fringed pools, in the open or even in forest. Often very abundant.

Distribution: Probably throughout continental Africa.

Trithemis hecate *Ris, 1912* (18)

This species prefers reedy pools and swamps or quietly flowing streams. Settles on reeds, sedges and grasses growing in the water.

Distribution: South Africa, Botswana, Zimbabwe, Mozambique, Zambia, Tanzania, DRC, Uganda, Cameroon, Chad, Mali.

Trithemis kirbyi *Selys, 1881* (18,8)

Usually settles on rocks or stones in the bed of fast or slow flowing stream and rivers in open country.

Distribution: South Africa, Namibia, Botswana northwards to equatorial Africa, Sudan, Ethiopia, India, Pakistan.

Trithemis monardi *Ris, 1919* (18)

Found on reedy pools or swamps, or sluggish reed fringed rivers.

Distribution: Angola, Zambia, Malawi, Mozambique, Zimbabwe, Botswana, Namibia.

Trithemis nuptialis *Karsch, 1894*

Normally a species of heavy forests, breeding in slow forest streams.

Distribution: Zambia, Angola, DRC, Uganda, W Africa.

Trithemis pluvialis *Förster, 1906*

Locally common species which settles on vegetation near or over running or slow-flowing streams.

Distribution: South Africa to Angola, DRC, E Africa.

Trithemis pruinata *Karsch, 1898*

Very local species which tends to fly in thick bush or forest near small streams.

Distribution: Central and Equatorial West Africa.

Trithemis stictica *Burmeister, 1839* (18)

Locally common in swamps, pools or streams in bush or open country or open forest areas.

Distribution: South Africa, Botswana northwards to Ethiopia and W Africa.

Trithemis weneri *Ris, 1912* (8)

Inhabits river valleys or low-lying plains. Generally settles on bare twigs of low bushes or other low plants near the river up to about 200 m from the river.

Distribution: Eastern half of Africa from Limpopo to Zambezi valley to S Malawi, rivers in lowlands of Kenya and Uganda.

Urothemis assignata *(Selys, 1872)* (18)

Common at reedy pools or streams.

Distribution: Natal, Mozambique, Zimbabwe, Zambia, Malawi north to Ethiopia.

Urothemis edwardsi *(Selys, 1849)* (18)

Prefers rivers or broad stream to pools.

Distribution: Natal, Mozambique, Zimbabwe, Botswana, Zambia northwards to Sudan.

Zygonyx atritibiae *Pinhey, 1964* (5)

Distribution: Zambia, DRC, Angola.

Zygonyx eusebia *(Ris, 1912)* (5)

One of the largest libellulids in the world.

Distribution: DRC, Angola, Zambia.

Zygonyx flavicosta *(Sjöstedt, 1899)* (5)

Distribution: DRC, Uganda, Angola, Zambia, W Africa.

Zygonyx natalensis *(Martin, 1900)* (18,5)

Usually very common at waterfalls and rapids.

Distribution: South Africa, Zimbabwe, Mozambique, Angola, DRC, Tanzania, Kenya, Uganda, W Africa.

Zygonyx torridus *(Kirby, 1889)* (18)

Distribution: Over most of continental Africa.

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CHAPTER 9 : APPENDIX 1
LIST OF ODONATA COLLECTED FROM BAROTSELAND

Odonata specimens were collected from the Barotseland area by Rafael Chiwanda and Philip Mhlanga from 20 March to 4 April 1999. Localities collected were:

Ndau School transect: 15°25'41"S / 22°57'49"E
 Ndau School area: 15°25'S / 22°58'E
 Sefula: 15°23'11"S / 23°10'07"E
 Mongu: 15°17'46"S / 23°08'36"E
 Kalabo: 14°58'10"S / 22°38'27"E
 Kalabo, 5 km west: 14°54'58"S / 22°34'02"E

List of Species Collected (nomenclature follows Pinhey).

ZYGOPTERA

Coenagrionidae

Agriocnemis exilis
 Agriocnemis sp.nr. exilis
 Agriocnemis sp.nr. falcifera
 Agriocnemis victoria
 Ceriagrion cf. glabrum
 Ceriagrion whellani
 Enallagma glaucum
 Pseudagrion coelestis
 Pseudagrion cf. coelestis (female)
 Pseudagrion sp. (female)

ANISOPTERA

Gomphidae

Crenigomphus sp.
 Ictinogomphus ferox

Cordullidae

Macromia bifasciata
 Macromia picta
 Macromia sp. (female)

Libellulidae

Acisoma panorpoides
 Acisoma sp.
 Aethriamanta rezia
 Brachythemis leucostricta
 Crocothemis erythraea
 Crocothemis sp.?
 Diplacodes deminuta
 Diplacodes lefebvrii
 Hemistigma albipuncta
 Olpogastra lububris
 Orthetrum brachiale
 Orthetrum cf. brachiale
 Orthetrum chrysostigma
 Orthetrum icteromelas cinctifrons
 Orthetrum trinacrium
 Palpopleura lucia
 Rhyothemis semihyalina
 Tholymis tillarga
 Tramea burmeisteri
 Trithemis annulata
 Trithemis hecate
 Trithemis kirbyi
 Trithemis sp.
 Urothemis edwardsi

CHAPTER 9 : APPENDIX 2 ODONATA SURVEY OF THE ZAMBEZI DELTA

Richard Kinvig

1. INTRODUCTION

The single most important cause of insect extinctions is the destruction of natural biotopes (Pyle *et al.* 1981). Wetlands world-wide are under the continuous threat of human disturbance. These disturbances include increased expansion of human populations, an increase in agriculture and the dumping of waste into waterways. In the past only a small amount of research has been done on the habitat preferences of African Odonata, yet it is known that several are under threat due to wetland disruption (Samways 1992).

Odonata, both adults and larvae, are valuable indicators of water quality and landscape disturbance (Watson *et al.* 1982, Castella 1987). They are good indicators due to their total reliance on water for their lifecycle and if the water quality is poor then the species will not proliferate. The water need not necessarily be polluted, but may have to higher silt load and therefore exclude the Odonata larvae. They are also an important and widespread component of freshwater ecosystems, being top predators (Corbet 1962). Many male Odonata are closely associated with particular biotopes (Steytler & Samways 1994). This may lead to exclusions, and therefore a range of biotopes are needed to suit the individual males and this is provided by large tracts of wetland.

Elliot Pinhey and some technicians from Bulawayo did the only work that has been carried out in this area in the early 1960s. Most of the expeditions into Mozambique were in the south, mainly to Maputo (Pinhey 1981). It was therefore important for us to get a collection of species for the area and then compare these to the previous collections done by Pinhey from 1947 to 1971 in the same area.

The study undertaken was to get information on the status and species list of the Marromeu complex, a wetland complex in the lower Zambezi Delta. The chosen sites are described with a brief history and description, for each of the species collected, and their distributions across Africa will be documented as well as their status.

2. SAMPLING SITES

The Odonata were collected using a sweep net and walking through the vegetation. The sampling was not done along transects. All species were captured in a random sampling of the sites.

2.1 Site A: Safrique

7/8 June 1999. 18°26'52" S / 35°53'46" E

Sampling took place in semi-cultivated lands, a short walk from the village of Safrique. The principle subsistence crop was rice and dominated the cultivated lands. The land was dry for the area and therefore the plants were small and shrivelled. In addition, but to a lesser extent was sorghum. In the grasslands adjoining the cultivated fields, the vegetation was made up mainly of *Vigna* spp., banana plants and Ilala palms (*Hyphaene coriacea*). The Ilala palms and the banana plants provided areas for the Odonata to shelter in. Where the *Pennisetum polystachion* grew to about 1.8 m high it provided shelter and retained moisture. The grass and Banana plants provided shelter for the predominantly more fragile species like *Ceriagrion glabrum* and other Zygoptera.

The larger Anisoptera could be found hawking over the open grass, examples of these being *Anax imperator* and *Crocothemis erythraea*. This area was sampled on two consecutive days and would fall into the class of "dry wet grasslands". The soil was a dry black loam that was very difficult to penetrate when so dry. Dry man-made channels traversed the cultivated lands.

2.2 Site B: Vila Nova

9/10 June 1999. 18°23'42" S / 35°54'27" E

Vila Nova is a small settlement 10 km from the town of Marromeu. It was sampled on two consecutive days. The area was wet with a small hand-dug canal approximately 3 m wide. On the one side of this canal was a settlement containing about 10 houses with the people dwelling in these houses, growing subsistence crops.

The crops comprised of rice, sugarcane, bananas, pineapples, coconuts and a very small amount of maize. In the Marromeu complex, crops and dwellings bound all water bodies. This therefore does not provide a true reflection of natural habitat for the Odonata, but they seemed to thrive in these environments. There was a small proportion of natural vegetation comprising *Pennisetum polystachion* and tall papyrus. It was difficult to sample "dry wet grassland", but in the end this area was deemed suitable. The main Odonata seen were *Orthetrum trinacria*, *Crocothemis erythraea* and *Trithemis arteriosa*. Again, *Ceriagrion glabrum* was prevalent for the damselflies. The species *Agriocnemis* sp. nr. *pinheyi* was found at this site for the first time. It was found around a well-sheltered clump of sugarcane.

2.3 Site C: River bank along the Zambezi 3 km range from Marromeu factory to Chinde
11 June 1999

The vegetation was typical of the habitat: *Eichhornia* spp., *Salvinia* spp. and *Ipomea* spp. Away from the waters edge at the high water mark there were stands of moribund grass. In and around the areas of human habitation and cultivation there were many species of weed including *Tagetes minuta*, *Senecio* spp., *Ageratum houstonianum* and *Bidens pilosa*. The sampling on this day was done from a canoe. It was done between 9:00 and 13:30. The areas sampled were specifically near the riverbanks, as no species seemed to be found over open water except for *Pseudagrion acaciae*. This is not very usual for species of damselflies as they are usually confined to areas that are well vegetated, and where the water is not flowing very strongly. *Trithemis annulata* was found integrating with *Crocothemis erythraea* and the two species of *Orthetrum* (*chryso stigma* and *trinacria*). This species of *Trithemis* seemed to be quite aggressive towards all other species of dragonfly. *Brachythemis leucosticta* was found in large numbers in and around a mud flat where they spent their time proportionately between hawking and sunning themselves. The *Pseudagrion* spp., *Ceriagrion* spp. and the single *Enallagma* spp. were found predominantly over the *Salvinia* spp. in the areas of backwater.

2.4 Site D: River bank, 4 and 6 km south of Marromeu 18°18'18" S / 35°59'58" E
12 June 1999. 18°19'51" S / 36°01'25" E

In both the 4 and 6 km sites there was no human habitation with the habitat being natural with open sand spits and areas covered with tall reeds and grass. In these two sites, the most commonly seen dragonfly was *Crocothemis erythraea* that could be seen hawking close to the vegetated areas of the spits. The dragonflies found were all fairly common to this type of habitat, except for one species that was recorded only once and was captured hawking over the grass on the island (*Neurogomphus uelensis*). No *Pseudagrion acaciae* were found and this may therefore infer that this species of damselfly has a relationship with *Salvinia* spp. as it was only near to it and on the adjacent open water.

2.5 Site E: Bambani Area 13 June 1999. 18°18'09" S / 35°53'21" E
This site can be described as "dry wet grassland". Small channels traversed the short grass, which made up this site. There were no species of special interest to be found here and the species that we did find could be called common to all areas studied.

2.6 Site F: Palm grove, north of Marromeu 14 June 1999. 18°13'05" S / 35°46'21" E
The palm-grove that we went to was completely disturbed by humans. Many of the palms had been cut done for use as canoes. The ground below the palms had been cleared, sorghum, and sugarcane planted in the place of the natural vegetation. There was also human habitation of the area and all the problems that go along with people, for example paths, large areas cleared around the houses and livestock. It was interesting to note, however, that the smallest damselfly in Africa (*Agriocnemis exilis*) could be found in the moribund areas of the sorghum and the sugarcane. The behaviour of the *Anax imperator* was as in Site A where it was hawking along the man-made paths.

2.7 Site G - Palm savanna, south of Marromeu 15/16 June 1999. 18°28'08" S / 35°53'43" E
Site Gilboa was situated 4 km south of Safrique and was sampled on two consecutive days as it was easily accessible and was the least disturbed site. Both coconut and ilala palms were in abundance and the grass growth was moribund. There were no channels or man-made canals and hence the site was very dry. This could explain the lack of Odonata as only one individual was found in the entire sampling period. The entire sampling period was six hours. This was broken into three and a half hours on the first day and two and a half on the second day.

3. SPECIES AND THEIR STATUS

The species found in the Marromeu area and their distribution across sampling sites are shown in Appendix 9.2 Table. 1. Each species is described below.

Agriocnemis exilis – Found throughout Mozambique. They are gregarious at reedy pools, swamps, sluggish streams. They make very brief flights and are fairly inconspicuous. Distribution: South to equatorial Africa, Madagascar, Mauritius and Réunion.

Agriocnemis sp. nr. *pinheyi* – This species has never been described before and therefore distribution and status are unknown.

Ceriagrion glabrum – This species has been found extensively throughout Mozambique and the rest of the Afrotropical region of Africa. Its status is common and was collected by Pinhey 50 km west of Marromeu.

Ceriagrion kordofanicum – The only records of this species previously recorded in Mozambique were by Moura, who found them at Vila Fontes in 1947. They were not previously seen in the Marromeu area. This species will only be found at low altitudes and on streams that have surface vegetation. They are found in Malawi, Kenya, Uganda and Sudan.

Enallagma spp. – The individual found was a female and further identification is impossible.

Ischnura senegalensis – The most common and abundant zygopteran. This species will be found all over continental Africa the islands and Asia. It will not be found in densely vegetated areas and is highly tolerant of saline waters. The absence of this otherwise common species, in the Marromeu complex is interesting since it is usually habitat non-specific. This lack of huge numbers could be due to seasonality. It must however be remembered that this is only an inferred reason and I have no proof.

Pseudagrion acaciae – This species is found on open water rivers with fast flowing currents and is seldom seen on small streams. It is found from Natal to Kenya, Zaire and Angola. It was recorded in Dondo and Chimoio by Pinhey in 1947. From the information available to me it does not look like it was recorded previously at Marromeu.

Pseudagrion coelestis – This species has only been found in Angola and Zimbabwe. There is no record of it having been recorded in the whole of Mozambique. There is also no description of its habitat, but when found it was close to the backwaters of the Zambezi that had surface vegetation. There is no record of its status, and it was uncommon in the study area.

Pseudagrion hamoni – Found in Mozambique, but not in the area that was studied by me. It prefers shady areas with lots of surface vegetation. In Mozambique, it has been found at Cabora Bassa dam. It is found from Zimbabwe to Kenya, Sudan and equatorial West Africa.

Pseudagrion helenae – This species has only been found in Northern Rhodesia (Bechuanaland). It was found under the same conditions as the above species. There is no mention of its status, but was uncommon in the study area.

Acisoma panorpoides – This is a common dragonfly that has been found all over Afrotropical Africa as well as Madagascar. It prefers quiet streams and stagnant pools with a surface vegetation of the type *Nymphaea*.

Anax imperator – This is a migratory species of dragonfly that is found throughout Africa, Europe and western Asia. It has a typical large dragonfly behaviour of hawking up and down slow moving rivers and open tracts of land.

Appendix 9.2, Table 1 Odonata species found in the Marromeu area, June 1999.

Family/Species	Site						
	A	B	C	D	E	F	G
ZYGOPTERA							
Coenagrionidae							
<i>Ceriagrion glabrum</i> (Burmeister, 1839)	X	X	X	X	X		
<i>Ceriagrion kordofanicum</i> (Ris, 1924)			X				
<i>Pseudagrion acaciae</i> (Förster, 1906)			X				
<i>Pseudagrion coelestis</i> (Longfield, 1947)			X				
<i>Pseudagrion hamoni</i> (Fraser, 1955)			X				
<i>Pseudagrion helenae</i> (Balinsky, 1964)			X				
<i>Ischnura senegalensis</i> (Rambur, 1842)			X	X			
<i>Enallagma</i> sp. (female)			X				
<i>Agriocnemis exilis</i> (Sélys, 1872)						X	
<i>Agriocnemis</i> sp. nr. <i>pinheyi</i>		X	X				
ANISOPTERA							
Gomphidae							
<i>Neurogomphus uelensis</i> (Schouteden, 1934)				X			
Aeshnidae							
<i>Anax imperator</i> (Leach, 1815)	X					X	
Libellulidae							
<i>Orthetrum chrysostigma</i> (Burmeister, 1839)			X		X		
<i>Orthetrum trinacria</i> (Sélys, 1841)		X	X				
<i>Palpopleura lucia</i> (Drury, 1773)	X	X			X		
<i>Hemistigma albipuncta</i> (Rambur, 1842)	X				X		
<i>Acisoma panorpoides</i> (Rambur, 1842)		X		X	X		
<i>Diplacodes lefebvrei</i> (Rambur, 1842)	X	X	X				
<i>Crocothemis erythraea</i> (Brullé, 1832)	X	X	X	X	X		
<i>Brachythemis lacustris</i> (Kirby, 1889)				X			
<i>Brachythemis leucosticta</i> (Burmeister, 1839)			X				
<i>Trithemis annulata</i> (Beauvois, 1807)			X				
<i>Trithemis arteriosa</i> (Burmeister, 1839)		X					
<i>Urothemis assignata</i> (Sélys, 1872)			X				
<i>Urothemis edwardsii</i> (Sélys, 1849)		X	X				X

Brachythemis lacustris – This species is gregarious at pools and rain puddles. Sometimes several individuals of the same sex are noted to sit on the same perch. This was noted when in the study area. They prefer open bush country from Mozambique to Ethiopia and West tropical Africa.

Brachythemis leucosticta – Recorded throughout Mozambique and Zimbabwe. It is scarcely disturbed by human intruders and this was noticed as sometimes one would stand on them while they were resting. They are found in most parts of Africa, southern Europe, Madagascar and western Asia.

Crocothemis erythraea – Very common dragonfly found in open country near streams, rivers and open expanses of water. It is found throughout Mozambique and Africa as well as Asia and Europe. It did not display any unusual behaviour or habitat preferences while observed.

Diplacodes lefebvreii – This species is common on pools or quiet margins of rivers, hence the reduction in numbers on the Zambezi itself, in open grasslands, in sparse or thick bush and even thin broad-leaved woodland. Nearly all of Africa and neighbouring islands as well as southern Europe and western Asia.

Hemistigma albipuncta – This is an abundant dragonfly. It often aggregates around open swamp, reedy or stagnant pools and is even common in forest. It may be dominant in the forests of Mozambique. It is found in most parts of Afrotropical Africa at lower elevations, except in Cape Province.

Neurogomphus uelensis – This species was first recorded in the Belgian Congo. This is all the information that can be found on it. I would therefore infer that it is a new species to Mozambique. It was found hawking over short grass near the Zambezi River.

Orthetrum chrysostigma – Found throughout central and northern Mozambique. It prefers open areas and does not venture into forest. It is highly tolerant of temperature gradients and pH gradients. It occurs in most parts of Africa and has a separate subspecies in Sierra Leone.

Orthetrum trinacria – Found to frequent still waters and mud pools. Found throughout Africa from Natal to Palaeartic North Africa. This individual species tends to fly low and for longer periods than other members of the genus. This behaviour was not noticed.

Palpopleura lucia – Found extensively in Mozambique. There are two forms and they may be found together, this not being the case in our study site. They prefer areas of swamp, reeds, grasses and twigs as these are used as perches. They are found in open country or bush and not forest. Where these individuals were caught supports this description, as does the resting on reeds, twigs and grasses. Found extensively throughout Africa.

Trithemis annulata – Found throughout Mozambique. As with the above species they were recorded by Pinhey at Marromeu. They are common in open bush, semi-arid zones, on rivers, streams, pools and swamps. All the areas mentioned by Pinhey were supported by my findings. They can be found throughout Africa, southern Europe and western Asia.

Trithemis arteriosa – This species is common to the majority of water bodies in Africa. It can usually be found all year round. They are highly tolerant of pH and temperature gradients. Most parts of Africa and western Asia.

Urothemis assignata – This species was last recorded by Pinhey at Marromeu in 1967, and has been recorded throughout Mozambique. It has a preference for reedy pools, lakes and sometimes swamps. It will always settle on the same perch even if chased away and this behaviour was noted. It sometimes hovers, but flies low. Natal to Ethiopia and equatorial Africa; also Madagascar.

Urothemis edwardsii – This is very similar to the above species but prefers more open expanses of water. Settles on high perches and is not readily driven away. Found 50 km west of Marromeu by Pinhey. Ranges from Natal to the Sudan, Angola and equatorial Africa and also Algeria.

4. DISCUSSION

There are only seven matching species in the review checklist and the 1999 survey. This may be ascribed to the fact that the checklist is from past records and was probably formulated from previous work done by Pinhey and the technicians from Bulawayo as well as Moura and the Ferreiras.

The more fragile species found in the 1999 study may be remnants from the summer and hence their low numbers and poor appearance (in terms of wing wear). The more fragile species include certain of the *Pseudagrion* and the *Agriocnemis* genus as well as the *Enallagma* genus. The one female *Enallagma* collected may be a remnant female which survived from the summer. The environment and the climate of this area do not vary much and can be described as semi-tropical. This allows for a higher survival rate of individuals throughout the year.

It must be said that the Odonata in general seem to have adapted well to changes brought about by man. In certain cases these anthropogenic influences may have helped the Odonata to increase their range as more micro-habitats have been created as a result. For example, the development of canals may provide corridors for the Odonata adults and larvae to move along as they are filled by natural streams and rivers. Both robust and fragile species co-exist and the numbers of certain species are extremely high. I would also postulate that at any time in the year there would be large numbers of Odonata, this being related to climate suitability and food availability.

In conclusion, the Odonata assemblage appears to be well represented and thriving, judging by the diversity of Odonata collected.

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CHAPTER 10

REVIEW OF WETLAND LEPIDOPTERA OF THE ZAMBEZI BASIN

Alan Gardiner

10.1 INTRODUCTION

The Lepidoptera is one of the largest insect orders with more than 150,000 species worldwide, of which more than 12,000 are thought to exist in Africa. The bright and attractive wings make them a familiar group to the general public. Adult Lepidoptera are readily distinguished from other insects by the presence of scales, often brightly coloured, on the wings, head and body. In all Lepidoptera, apart from a few of the more specialized families, there is a spur-like structure (an epiphysis) on the fore tibia, a structure that does not occur in other insects. Together with the way in which the mouthparts are modified to form a coiled, sucking tube (proboscis), this is characteristic of the group (Henning 1985).

The attractiveness of butterflies and larger moths has given them considerable appeal amongst amateurs. Because of collecting and research by these amateurs and a few professional entomologists, butterflies are now perhaps the best known invertebrate group in terms of both taxonomy and distribution. This, in addition to other biological traits, makes them an important group for biodiversity studies. These traits are:

- (a) the group is sensitive to changes in the environment,
- (b) large numbers may be present, so that time spent in the field quickly yields a substantial data set,
- (c) families that are relatively easy to identify can be selected, and for some regions detailed taxonomic information is available,
- (d) they can be collected in a quantitative manner.

There are many Lepidoptera of economic and social importance. They have an obvious agricultural importance, both as pests and pollinators, but some species are also valued as food. For example, the larva of a Saturnid moth, the mopane worm (*Imbrasia belina*), is collected and dried for human consumption and is a common part of the human diet from the northern half of South Africa through to central Zambia. Another emperor moth larva eaten throughout the Zambezi basin is *Cirina forda*. Around Victoria Falls, the branches of one of its larval food plants, *Burkea africana*, are broken in order to collect the caterpillars. The importance of lepidopteran larvae as food has often been written about, for example Chavanduka (1975) illustrated the importance of insects as a source of protein, Defoliart (1995) reviewed "edible insects as mini-livestock", and Roberts (1998) states "There is little doubt that the emperor moth *Gonimbrasia* [*Imbrasia*] *belina* is one of the major economically important insects in Southern Africa". In some parts of its range the cost of this insect per kilogram is more than the price of dried meat.

This chapter firstly reviews existing information on the Zambezi Basin (Section 10.3), covering the major works on Lepidoptera and collections from the area. Taxonomy and taxonomic works are not covered. In the next section (10.4), the Zambezi River itself is divided into six faunal sections. Species recorded from each section and any noticeable and obvious features of the fauna are given.

Thirdly, in Section 10.5, the wetland species occurring along the Zambezi are discussed. For each species, information on its diagnosis, habitat, habits, conservation status and distribution is given. Finally, in Section 10.6 the faunal regions are discussed from a biogeographical viewpoint.

10.2 HIGHER CLASSIFICATION

Butterflies were regarded as a suborder of the Lepidoptera – the Rhopalocera or 'club-horned' – to distinguish them from the suborder Heterocera, or 'varied-horned', moths. Today, the differences between butterflies and moths are considered so slight that this division is no longer justified (Skaife 1979). Most butterflies are brightly coloured, the tips of their antennae are swollen and they fly by day. The caterpillars are seldom hairy, although some are armed with spines. Also, with the exception of some of the more primitive species, the pupae are not enclosed in cocoons. A more fundamental difference between butterflies and moths is that the wings on each side of a butterfly are not linked together by a jugum or a frenulum – except, again, in a few of the most primitive species found in Australia. Instead, at the front of the hindwing there is a rounded lobe, known as the humeral lobe, which presses against the underside of the forewing when the insect is in flight.

Butterflies form two superfamilies – the Hesperioidea, comprising one African family (the Hesperidae), and the Papilionoidea with five families (the Nymphalidae, Pieridae, Lycaenidae, Riodinidae and Papilionidae). The Hesperioidea differs from the Papilionoidea in having the antennae set widely apart at the base, and the peripheral veins of both wings are not stalked.

10.3 EXISTING INFORMATION

This review principally focuses on butterflies as meaningful conclusions can be drawn from this group. Emperor moths are also mentioned, but unfortunately only general distributions of this group are available as it has not been collected to the same extent. Although Pinhey (1962) has described the hawk moths of central and southern Africa, and d'Abrera (1986) has published *Sphingidae Mundi*, the taxonomy and distribution records for the group are still poor. Important emperor moth records are mentioned in the appropriate section.

Most of the data in this review has been collected by amateur butterfly collectors. Some of this information is available as checklists, but more detailed information is housed in private collections. There are several large private collections. Those relevant to the Zambezi Basin are: (a) Steve Collin's collection, now known as ABRI (African Butterfly Research Institute) in Nairobi, Kenya. This also contains Alan Heath's Zambian collection and collections from Zambia and Malawi by Ivan Bampton, Colin Congdon and Ray Murphy; (b) C.B. Cottrell's collection housed in Harare, and (c) the Gardiner collection, housed in Bulawayo. Some smaller collections are those of the late Rob Pare housed in Bindura, and Ian Mullin's collection housed in Harare. The Natural History Museum of Zimbabwe in Bulawayo also has a fine collection of specimens from south central Africa, to which many collectors have contributed. Of particular note are the collections of E.C.G. Pinhey. The collections of Rob Pare and half of the Gardiner collection have been put onto an electronic database.

There are noticeable gaps in collecting along certain parts of the Zambezi, in particular from where the Zambezi leaves NW Zambia and enters Angola downstream to Katima Mulilo. A small amount of collecting has taken place at Zambezi and Lukulu, but these collections are in the UK and not

available for study. There has also been little collecting from Luangwa through to the Zambezi Delta.

Carcasson's (1995) *African Butterflies* provides the most recent information on the taxonomy of African butterflies, and nomenclature used in this review follows this. Apart from d'Abrera (1980, 1997), *Butterflies of the Afrotropical Region*, there are no references that cover the butterflies of the Zambezi Basin. Field guides such as Migdoll (1988) and Williams (1969) cover only a limited number of species. Evans (1937) provided a catalogue of the African Hesperidae housed in the British Museum, while Henning (1989) published a comprehensive book on the Charaxinae butterflies of Africa. Another significant work is that by Ackery and Vane-Wright (1984) on milkweed butterflies of the world which provides useful taxonomic and ecological information on the African species. The fauna of various parts of the basin is covered by a number of books and publications, of which the most important are given below. Checklists for Zambian butterflies are given by Neave (1910), Denning (1979) and Heath (1982), while Pinhey and Loe (1977) provide a small guide to some of the species. Heath is about to publish a checklist of Zambian butterflies using the collections of Denning (early 1950s), Cottrell (late 1950s), Pinhey (1970s), Heath (late 1970s), Gardiner and Blease (1980s), Terblanche (1990s), and Bampton and Congdon (late 1990s). The most useful information on the butterflies of Zimbabwe and Mozambique is given in Pennington (1978, 1994), *Butterflies of Southern Africa*. This text includes a few keys and relies on its colour plates for species identification; it also includes country-based distributions. The first volume, on the Hesperidae, Papilionidae and Pieridae, of a series of five on butterflies of southern Africa has recently been published (Henning *et al.* 1997), but this excludes those species that are not found in South Africa. Other texts that provide information on species found in Zimbabwe include Cooper (1973), Murray (1935), Pinhey (1949a, 1949b, 1965) and van Son (1949, 1955, 1963, 1979). Torben Larsen (in prep.) compiled a checklist to the butterflies of Botswana, and it is from this that most of the Chobe records given here are taken. In addition to many other localities, Torben's checklist contains most of the information collected by Pinhey (1968, 1971, 1972, 1974). In the 1960s and 1970s Pinhey carried out a significant amount of collecting in the Victoria Falls area, the results of which are presented in Pinhey (1975). The most significant published information available for the butterflies of Malawi, which also covers the Zambezi to a limited extent, is that by Gifford (1965). This provides a keyed checklist to the Malawi butterflies and colour plates.

10.4 ZAMBEZI FAUNAL REGIONS

The Zambezi Basin covers a vast geographical area, and it is not possible, with the present resources, to cover the entire basin. In this preliminary study, the Zambezi River is looked at from its origin in northwestern Zambia through to the delta on the Mozambique coast. An attempt has been made to divide the river into six faunal sections. The dividing line between sections is not clear-cut, although the separation is logical and based on habitat differences – a combination of geographical and floristic factors.

The fauna described for each section, apart from the first, are those species recorded from the vegetation in or alongside the Zambezi. If only wetland species were being considered, little difference would be found between the different sections of the Zambezi, with the possible exception of the first. The main factors separating butterfly faunas along the Zambezi are probably climatic conditions and the type of woodland, and not the presence of wetlands.

For the first section, the tributaries near the source of the Zambezi and their associated dambos have been included. Lepidoptera from other tributaries of the Zambezi have not been included, except for the Chobe and part of the Lower Shire. More detailed work on the Lepidoptera of the Zambezi Basin as a whole is being carried out by WWF in Harare. For each faunal region, important or noticeable species and features of the fauna are noted, along with species of conservation concern. A list of all species recorded from the Zambezi River area is given in Table 10.1 (at the end of this review).

10.4.1 Section 1: Northwestern Zambia and the neighbouring part of Angola

The northern border of Zambia is influenced by two river systems, that of the Congo and that of the Zambezi. The northern Zambian border is in fact a watershed which separates the waters of the Congo from those of the Zambezi. All the rivers and streams immediately to the north of the border fall within the catchment of the Lualaba River, which eventually becomes the Congo. Evergreen riverine forest stretching back to the great central rainforest of Africa extends close to Zambia's northern border, and the longest tributary of the Lualaba reaches right to the border of northwest Mwinilunga, a very short distance from the source of the Zambezi. Hence there is a strong influence from the central forest block, and many of these species occur in this region of Zambia, for example species from the genera *Charaxes* and *Euphaedra*.

The Zambezi has its source in Mwinilunga at an altitude of approximately 1370 m altitude. This first part of the Zambezi, around Kalene Hill, has an unusually rich fauna with many species also occurring on eastern tributaries of the Zambezi headwaters. Many expeditions resulting in good collections have been made to this area (e.g. Denning, early 1950s; Cottrell, late 1950s; Pinhey, 1970s; Heath, late 1970s; Gardiner and Blease, 1980s; Terblanche, 1990s).

The rainforest biome contrasts strongly with the surrounding deciduous or semi-deciduous forests that cover much of Zambia. In general, the influence of the main Congo rainforest zone extends across the north of the country in the form of strips or patches of riverine, evergreen, moist forest, including swamp forest. The richness of the fauna of the area surrounding the source of the Zambezi is principally due to the forest along its margins.

These forests influence the butterfly fauna in two ways. They provide specialized microclimates, and they provide a different range of host plants. Thus species which require the deep shade of the forest floor are common in the forests near Kalene Hill. Plant families common there, such as Lauraceae, are hosts for species such as *Papilio hesperus*. Riverine evergreen habitats also exist to a limited extent in other parts of the country, and here butterfly species occur which prefer evergreen hostplants not normally found in savanna habitats.

In many of the northern riverine habitats, the occurrence of rainforest fauna is patchy, with each patch differing in its species composition. For example, along a small, shady stream, one may see the White Banded Swallowtail (*Papilio echerioides homeyeri*), the small Riodinin (*Abisara rogersi*) and possibly Euthaline forest floor species (e.g. *Aterica galene* and *Catuna crithea pallidior*). In contrast, in another patch the unusual lycaenids *Dapidodigma demeter nuptus* and *Argyrocheila inundifera* may be found.

Wet, thickly forested areas at the sources of streams may contain unusual species. The source of the Zambezi, some miles north of the Mwinilunga–Ikkelenge road, is home to deep shade species of the forest floor such as *Bicyclus sebetus*, *B. trilophus* and *B. sophrosyne overlaeti*. The Zambezi source has also provided a record of the rare and beautiful *Charaxes acuminatus cottrelli*. Not far away,

near the Ken Suckling Mission on the Luakela River, Blease found the only known Zambian colony of the African Leaf Butterfly, *Kamilla ansorgei*, in April 1988. Similar habitats occur in the northern Luapula Province, for instance along the Kalungwishi River and in Northern Province. Here, *B. sebetus* also occurs, together with unusual *Charaxes* such as *C. lucretius schofieldi* and *C. eudoxus zambiae*.

Of all these habitats, the most notable is the Isombo and Mudileji cluster of streams to the west of Kalene Hill which flow into the Zambezi inside Angola. These forests are not connected to the Congo rainforest to the north, and appear to represent a relict fauna from past pluvial periods. First noted in 1954, these relatively small evergreen areas had been undisturbed throughout the colonial period due to their proximity to the Angolan border; by mutual agreement people could pass through them but not settle within them. They survived intact until the 1970s, but their status today is not clear owing to a large influx of refugees from Angola. It has been reported that the Isombo forest has been cut down to make way for cassava fields and fish ponds. Thus, an appreciable number of species listed in Table 10.1 may no longer occur within Zambia. However, if there are other relict patches in the same neighbourhood, these species may still survive.

A common swallowtail butterfly in these forests is the green *Papilio phorcas congoanus*, otherwise recorded only from Mufulira and the Kalungwishi. It reoccurs as a different subspecies *P. p. nyikanus*, far to the east in the Afromontane forests on the Nyika Plateau. The subspecific differences suggest an absence of widespread interconnected gene flow since before the last northern glaciation and its contemporary arid period in Central Africa (possibly 22,000 BP). Other notable Swallowtails are the large *Papilio hesperus* and *Graphium ridleyanus*, a remarkable reddish *Acraea* mimic.

Among the Pieridae, the unusual delicate, translucent-winged *Pseudopontia paradoxa* is so distinctive it has been placed in its own monotypic subfamily. This species was bred for the first time by Heath (1977), who observed specimens laying on the plant *Rhopalopilium marquesii* growing along the Jimbe River. There are two subspecies – *P. paradoxa paradoxa* occurs in forests from Sierra Leone through to the northern Democratic Republic of Congo (DRC), and *P. paradoxa australis* occurs in central and southern DRC, Angola and northwestern Zambia. It is suggested *Pseudopontia paradoxa australis* is placed on IUCN's list of Vulnerable species because of its close relationship with riverine vegetation and unique taxonomic status. Another two wet forest pierids are *Leptosia hybrida vansomereni* and *L. nupta*.

Large acraeine species found in the forest are *Acraea epaea*, *A. macarista* and *A. umbra macaroides*, while common danaines are *Amauris niavius* and *A. tartarea*. The satyrines *Gnophodes betsimena parmeno*, and the previously mentioned *Bicyclus* species, as well as *B. mesogena*, *B. mandanes* and *B. dubia*, occur in deep shade.

The family Nymphalidae are represented by *Lachnoptera anticlea*, *Kamilla cymodoce*, several forest *Neptis* species (e.g. *N. nemetes*, *N. nicoteles*) and the common *Pseudoneptis bugandensis ianthe*. The splendid scarlet male of *Cymothoe sangaris luluana* may be seen after the rains sunning itself on leaves near the Isombo River, and in the deep shade one may see *C. herminia katshokwe*. The splendour of these are matched by large *Pseudacraea*, such as *P. kuenowi*, *P. boisduvali*, *P. lucretia protracta* and the smaller green spotted *P. semire*. Three dark purple-blue forest floor species of *Euriphene* (*E. pallidior*, *E. incerta theodota* and *E. saphirina trioculata*) may sometimes be found in large numbers flying alongside *Catuna crithea pallidior* and *Aterica galene*. Even more spectacular in the understorey are the large purple, yellowish, orange and reddish *Euphaedra* such

as *E. overlaeti*, *E. herberti katanga*, *E. katangensis*, *E. cooksoni*, and *E. crawshayi*. The Isombo area has eight *Euphaedra* species. These fly from ground level to shoulder height, while the four *Bebearia* species, particularly the large and striking *B. plistonax*, tend to skim the ground.

Notable lycaenids fluttering in the shade are the white *Oboronia guessfeldti* and the delicate hairstreak *Oxylides faunus*. The very large hesperiid *Gamia shelleyi* may be seen flying along the streams. In July, well into the dry season (and normally only found in Cameroon and the DRC), the rare *Artitropa cama* appears.

There are also many spectacular rainforest species of the genus *Charaxes* belonging to the *Tiridates* group, notably *C. numenes aequatorialis*, *C. tiridates tiridatinus*, *C. imperialis lisomboensis*, *C. ameliae amelina* and *C. pythodoris*. Rainforest *Charaxes* of other groups include *C. eudoxus* (which occurs in Zambia as three subspecies), *C. lucretius* (two subspecies), *C. anticlea proadusta*, *C. hildebranti katangensis*, and the black *C. etheocles carpenteri* and *C. cedreatis*. While virtually all of these species are found in the strips of evergreen forest at Kalene Hill, many also occur in other forest patches across northern Zambia.

In this northern region of Zambia there are species, such as *Acraea mirifica* and *Zeretis fontainei*, restricted to marshy areas. A number of other acraeines, although not found exclusively in marshy places, prefer them. Two species quite tightly linked to marshes are *Acraea rahira*, which feeds on Polygonaceae, as well as on *Erigeron* (Asteraceae), and *A. ventura* which utilises *Cassia* plants. Less closely linked to marshes are *A. acerata* and *A. periphanes*, both of which utilize a range of herbaceous and shrubby host plants. Other nymphalids that are mainly seen in marshy places are *Junonia ceryne*, *Neptis jordani* and the False Fritillary, *Pseudargynnis hegemone*.

A number of emperor moths can be found in northwestern Zambia. One species only recorded from this region is Kuhne's Lunar Moth, *Argema kuhnei*. The genus *Argema* is the well-known group of Moon or Lunar Moths; these moths produce a silky cocoon. They are yellow or green in colour with very long hindwing tails; *Argema kuhnei* has a chrome-yellow ground colour with some greenish yellow basal tints. It is also likely to occur in the Shaba Province of the DRC, although it has not yet been recorded there.

From northwest Zambia the Zambezi flows southwest into Angola and has no direct connection with the Lualaba catchment. No collections from this part of Angola have been noted and we have no idea of the ecological state of the riverine forests. Having passed in a wide arc through Angola, the Zambezi re-emerges to form the Barotse Plain.

10.4.2 Section 2: Barotse Floodplain

Apart from collections made by C.B. Cottrell and a small recent collection by the BFA, very little collecting has taken place in this area. At Mongu, Cottrell recorded a rare and interesting species, *Erikssonia acraeina* (for notes on its ecology see Henning 1984). This species is on the IUCN list of Vulnerable species and only a few scattered populations have been found in central and southern Africa. Although not a swamp species, being found on the higher ground at Mongu, it would be of interest to know if it still occurs in this area. Its food plant is *Gnidia kraussiana*.

Most of the species recorded from this section are either wetland species (such as *Neptis jordani*, *Leptotes pulcher* and *Acraea acerata*) or common migrants (for example, *Belenois aurota*). *Mylothris rubricosta*, unlike many of this mistletoe-feeding genus, uses herbaceous Polygonaceae as their food plants. It is a true marsh species.

One group of emperor moths found in this section of the Zambezi are those belonging to the genus *Bunaepsis*. These are normally brightly coloured moths with yellow and red background colours and black stripes. They have well developed eyespots on both the fore and hindwings. The larvae are usually adorned with short thick spines and feed mostly on sedges and grasses.

10.4.3 Section 3: Senanga to Victoria Falls, including the Chobe/Linyanti swamps

After leaving the Barotse floodplain towards Victoria Falls, the Zambezi passes through dry forests on Kalahari sands. Some information is available for species collected just above Victoria Falls at Kazungula by Pinhey in the 1960s and 1970s, and there is reliable information available for the Chobe system (Larsen, in prep.). Amongst the few species of interest in this area, the most important are the true marsh species, *Mylothris rubricosta* and *Leptotes pulcher*, dealt with later. Most species from this section have wide distributions, but a few, such as *Acraea atergatis* and *A. atolmis*, are linked to the Kalahari sand system. These two acraeas are particularly common in the Livingstone-Victoria Falls area, through the northwestern part of Zimbabwe and west through Botswana to Ovamboland in Namibia.

Because of the microclimate produced by the Victoria Falls, some interesting taxa occur in the "rainforest". The rainforest fauna is noticeably different to that of the surrounding area. Of particular note is the unusual *Acraea anemosa* form *albiradiata*, which has only been taken in this forest and at Katima Mulilo in Namibia. Nothing is known about the population at Katima Mulilo, but at Victoria Falls the population is Conservation Dependent (cd). This taxon with its limited distribution (only two small populations being known), should be given special conservation status. Other species found at Victoria Falls are listed by Pinhey (1975).

Within the forest there are some large and attractive butterflies. The genus *Papilio* is represented by *Papilio nireus lyaeus*, with its black background and blue or green bands, the common and widespread *P. demodocus*, which is mainly black and yellow in colour, and *P. constantinus*, a black and yellow species similar to *P. demodocus* but with tails. In and outside the forest one will also come across *Graphium leonidas*, *G. antheus* and *G. porthaon*, the latter two have very long and attractive swordtails on their hindwings. This is one place where *Graphium porthaon* can be found in large numbers; its food plant, *Friesodielsia obovata*, is common in the surrounding Kalahari sands. The other noticeable large species is the white *Nephronia thalassina*. The male flies quite rapidly and is a delicate pale blue in colour, while the female is a slower flier and is either off-white in colour or, in form *sinolata*, has an attractive yellow hindwing. This seems to be the commoner form at Victoria Falls. The Clouded Mother-of-Pearl, *Salamis anacardii nebulosa*, is a large attractive Nymphalid that can be found inspecting the understorey bushes.

Recently, Henning and Henning (1994) described *Charaxes zambeziensis* from the Victoria Falls. However, it is likely that this species is not valid as the male is probably *Charaxes vansoni* while the female is probably *C. fulgarata*, the female of which has many attractive forms. Some have blue hindwings with blue and black forewings, while others have blue hindwings with blue, white and black forewings, while yet others have a whitish blue hindwing with light blue and black forewings. The food plant of *C. fulgarata* is the tree *Amblygonocarpus andogensis* which is common in the vicinity of the Falls. There is a fine specimen of this tree outside the Victoria Falls railway station, at times females can be seen ovipositing on it.

The genus *Acraea* is also common in the rainforest and surrounding bush. In fact, four species were described from specimens caught near the Falls – *A. atergatis*, *A. atolmis*, *A. axina* and *A. aglaonice*

were all described by Westwood in 1881. Of these, *A. atolmis* is particularly noticeable during the dry season as the male is bright scarlet in colour.

An interesting record from the Palm Grove area of Victoria Falls is an attractive little lycaenid *Spindasis brunnea*. Two specimens were taken in 1938 by R.W. Barney and are the only records for southern Africa. As there are records in the British Museum of *S. brunnea* from Ndola, also caught by R.W. Barney but in 1941, it is possible that the 1938 specimens were labelled Victoria Falls by mistake.

Ypthimomorpha itonia, the Swamp Ringlet, is common in the surrounding swampy areas. Another small ringlet, *Ypthima cataractae*, was described from the Victoria Falls by van Son in 1955. It has, however, been synonymised with *Y. granulosa* (Kielland, 1982) which is found in grassy and swampy areas from East Africa through to Zimbabwe. The other wetland species that have been recorded from the Falls are *Acraea acerata*, *Catacroptera cloanthe*, *Mylothris rubricosta* and *Eicochrysops hippocrates*. Other wetland species that should occur there are *Acraea rahira*, *Neptis jordani*, *Leptosia alcesta*, *Cacyreus lingeus*, *Cupidopsis cissus*, *Leptotes pulchra* and *Parnara monasi*.

10.4.4 Section 4: Victoria Falls to Tete

The butterfly fauna from the gorges below Victoria Falls through to Tete is typical of more hot, arid areas. This section could be divided into two subsections – the area above Kariba dam wall and the part below. Below Kariba dam, the Zambezi is joined by the Kafue River at an altitude of around 500 m, and then by the Luangwa River at Luangwa at around 370 m. A list of butterflies collected from Cabora Bassa by M.C. & G.V. Ferreira is given in Pinhey (1976).

The presence of Pieridae, or Whites, is a noticeable feature of this section of the Zambezi Valley and it is common to see massive migrations of this group. The species normally involved are *Catopsilia florella* and *Belenois aurota*. With these one may find other species such as *Graphium porthaon* and *Phalanta phalantha*. The migrations normally happen during the early months of summer, and the butterflies fly from north-west to south-east.

Another White that catches the eye is *Nephronia argia*, with its peculiar underside markings. The hindwing underside is a deep yellow in colour, while the forewing underside is white with the basal half a red-orange colour. It is a rapid flier and only when perched can the underside colouration be seen; in flight the white uppersurface shows. *Eronia leda* is also common; the male is bright yellow in colour with an orange tip, while in the wet season the female is almost completely yellow (in the dry season it also has an orange tip).

The genus *Colotis* is well represented in this section, with its variously tipped forewings. Examples are *C. vesta*, *C. celimene amina* (male with its crimson streaked wingtips), *C. ione* (male with purple wingtips), *C. danae annae* (male with its scarlet apical patches), *C. antevippe gavisa* (male with its reddish-orange apices), *C. eris* (male with golden apical spots), and *C. euipe mediata*, *C. pallene* and *C. evagore antigone* (the smaller yellow or orange-tipped *Colotis*). Most of these species are fairly widespread. A particularly widespread species is the small *C. amata*, which is also found in hot, dry places in south Asia. Similarly, the Zebra White (*Pinacopteryx eriphia*) is found almost everywhere in drier localities. The small white *Nepheronia bucqueti* occurs in open places, while the large satyrine *Melanitis leda* can be found commonly in the shady ravines or thickets.

Between Chirundu and Kanyemba, Hancock (in the 1980s) and Gardiner (in the 1990s) have recorded the rare *Dixeia leucophanes* in thickets, a species restricted to this region, low-lying areas in Mozambique and parts of the Sabi Valley in Zimbabwe. It is a medium-sized white butterfly and a rapid flier. Many Whites fly together with *D. leucophanes*, including its close ally *D. doxo*.

In the Mana Pools area in thick riverine bush, especially along the small rivers that enter the Zambezi, some beautiful *Charaxes* can be found. The most spectacular of these is *Charaxes cithaeron joanae*. The male has bright iridescent blue spotting on the forewing upperside, while the hindwing upperside has a large pale blue discal patch. The female has a wide and solid white discal band on the forewing, and the hindwing has a large blue-white discal patch. Another common *Charaxes* is *C. ethalion binghami*, one of the Black *Charaxes*.

The only wetland butterfly species to have been recorded from this section are *Catacroptera cloanthe*, *Leptosia alcesta* and *Leptotes pulcher*. It is likely there will be fewer wetland species here compared to other sections, but others that should be found are *Ypthimomorpha itonia*, *Acraea rahira*, *Cacyreus lingeus*, *Eicochrysops hippocrates* and *Parnara monasi*.

A rare emperor moth, the Frog Foot *Antistathmoptera daltonae*, has been collected from Chirundu. It is a large orange-brown species with very long tails which are even longer than those of the Moon Moth. Of the two subspecies, the typical *A. d. daltonae* is from the Usumburu mountains in north east Tanzania, while the Chirundu subspecies, *A. d. rectangulata*, has also been recorded from low altitude forest in Mozambique and Malawi.

10.4.5 Section 5: Tete to Mopeia

Below Tete and closer to the Zambezi Delta, the Shire River enters the Zambezi. Although little collecting has taken place in the Lower Shire marshes, the following marsh species have been recorded: *Neptis jordani*, *Catacroptera cloanthe*, *Junonia ceryne*, *Leptosia alcesta*, *Cacyreus lingeus* and *Parnara monasi*. Some information on this area can be found in Gifford (1965). In highland areas further up the Shire and its tributaries, such as Cholo and Zomba, there are many endemic and interesting species. For instance, on Cholo Mt. *Eretis herewoodi* is only found in marshy glades near forest.

10.4.6 Section 6: Zambezi Delta

There appears to have been no collecting in this area except for a recent trip carried out by this project. As the field trip was done late in the season and a poor species list was obtained it is difficult to draw any conclusions. Most species collected were eclectic which may indicate: (a) the area is much disturbed and modified by human activity, (b) due to the time of year only common and obvious species were present, and/or (c) only the conspicuous species were caught. If the low species count is due to human impacts there may be concern for the environmental health of the area. Of the species recorded from the area, a few, such as *Euphaedra neophron*, confirm the link the area has with the eastern forests and woodlands. Four wetland species were collected: *Eicochrysops hippocrates*, *Ypthimomorpha itonia*, *Neptis jordani* and *Parnara monasi*. At least an additional six species should be found: *Leptosia alcesta*, *Leptotes pulcher*, *Cacyreus lingeus*, *Cupidopsis cissus*, *Acraea rahira* and *Catacroptera cloanthe*.

10.5 WETLAND SPECIES

Species listed as wetland species are those that have a close relationship with wetlands. Most are dependant on swamp plants such as *Polygonum* as larval food, and therefore only occur within or very close to swamps (for example, *Mylothris rubricosta*). Some wetland species, such as *Catacroptera cloanthe*, may be found in other moist habitats. The habitat and habits of each species give an indication of how tightly bound the species is to the swamp or wetland habitat. A list of butterflies considered to be wetland species is given in Table 10.2.

Over the rest of Africa there are only about 15 additional wetland, swamp or marsh associated species – *Mashuna mashuna* occurs in high level dambos on the Zimbabwe highveld; *M. upemba* occurs in dambos in the Shaba Province of the DRC, SW Tanzania and Angola; *Acraea bettiana* occurs in swamps above 2100 m in western Uganda, Rwanda, Burundi and eastern DRC; *A. rangatana* occurs in swamps above 2100 m in Kenya, Rwanda to Uganda and eastern DRC; *A. odzala* is found in the DRC; *A. hecqui* in south Kivu, DRC; *A. pierrei* in north Kivu, DRC; *A. guichardi* in western Ethiopia; *A. necoda* in the Ethiopia highlands; *Metisella meninx* in wet meadows in South Africa; and *M. midas* in high level dambos in eastern Africa. The following species of *Pseudonympha* are restricted to marshy ground in high mountainous regions – *P. varii* and *P. swanepoeli* in South Africa and *P. cyclops* and *P. arnoldi* in eastern Zimbabwe.

The health of a wetland can be indicated by the presence or absence of certain species, particularly if one takes into account the abundance of the component species. A sudden decrease in numbers of a species, if change due to climatic conditions can be ruled out, can be a warning that there has been a marked change in the environment. Other groups such as dragonflies and mayflies, however, may be better indicators of water quality.

10.5.1 Species Descriptions

1. *Leptosia alcesta inalcesta* Bernardi, 1959

African Wood White

Diagnosis: This flimsy white butterfly is easily identified in our region by its black tip and black postdiscal spot.

Habitat & habits: It has a distinctive slow bouncing flight. Found in many different shady habitats from forests to riverine thickets in low hot valleys, it is seldom or never found far from water. Its favoured habitat is along rivers. Though on the wing throughout the year, it is generally more plentiful in late summer and autumn.

Conservation status: Although its numbers may be influenced by human impact, it is unlikely to be under any threat.

Distribution: The species has a wide distribution occurring from the Natal coast, through Zimbabwe and Zambia to East Africa. A different subspecies is found in West Africa. It may be found along the whole length of the Zambezi.

Food plants: *Capparis brassii*, *C. fascicularis* (Pennington 1994), *C. tomentosa* and *Maerua juncea* (Henning *et al.* 1997).

2. *Mylothris rubricosta rubricosta* (Mabille), 1890

Swamp or Papyrus Dotted Border

Diagnosis: This and the next species are readily recognized by their white colour and the costa on their under and upperside being bordered by a distinctive orange streak (hence the specific name *rubricosta*). In the past *M. rubricosta* was considered to be a subspecies of *M. bernice*, but in *M. rubricosta* the marginal forewing spots are not produced along the veins, while in *M. bernice* the marginal spots along the costa project inwardly along the veins.

Habitat & habits: The larval food plant (*Polygonum*) is intermixed with papyrus, so the butterfly often lives completely away from dry ground. The flowers of *Polygonum* are a favourite nectar source for the species. Records are from August to April. The flight is light and floating with an occasional fluttering movement; it always flies low down and often amongst the reeds. Seldom seen more than a few metres away from its swamp habitat.

Conservation status: Low Risk, least concern.

Distribution: There are two subspecies, one in eastern and southern Africa from Ethiopia through to Zambia, Angola, northern Botswana, northwestern Zimbabwe and Malawi, and a second subspecies in the east of the DRC. Within the Zambezi Basin, this species is widespread (although localised) along the Zambezi above the Victoria Falls and along the Kafue, while in Malawi it will probably be found in the Lower Shire. In Botswana it is only known to occur in the panhandle of the Okavango and in the northwestern part of the delta, but is also likely to occur in the Kasane area since there are records from the Kazungula Rapids just inside Zimbabwe.

Food plants: *Polygonum* spp. (Polygonaceae), and on *Polygonum barbatum* in East Africa.

Table 10.2. Wetland Lepidoptera species from the Zambezi Basin.

Family Pieridae	Acraeinae
Pierinae	11. <i>Acraea rahira rahira</i>
1. <i>Leptosia alcesta inalcesta</i>	12. <i>A.ventura ventura</i>
2. <i>Mylothris rubricosta</i>	13. <i>Acraea mirifica</i>
3. <i>Mylothris bernice</i>	14. <i>Acraea acerata</i>
	15. <i>Acraea periphanes</i>
Family Lycaenidae	
Polyommatainae	Nymphalinae
4. <i>Eicochrysops hippocrates</i>	16. <i>Catacroptera cloanthe</i>
5. <i>Leptotes pulcher</i>	17. <i>Junonia ceryne ceryne</i>
6. <i>Cacyreus lingeus</i>	
7. <i>Cupidopsis cissus</i>	Limenitinae
	18. <i>Neptis jordani</i>
Theclinae	19. <i>Pseudargynnis hegemone</i>
8. <i>Zeretis fontainei</i>	
9. <i>Zeretis sorhagenii</i>	Family Hesperidae
	Hesperinae
Family Nymphalidae	20. <i>Parnara monasi</i>
Satyrinae	21. <i>Borbo micans</i>
10. <i>Ypthimomorpha itonia</i>	

3. *Mylothris bernice overlaeti* Berger, 1981

(no common name)

Diagnosis: See preceding species for identification.

Habitat & habits: Also an inhabitant of swampy areas.

Conservation status: Vulnerable.

Distribution: There are five subspecies of this butterfly. The nominate subspecies is from Gabon and Cameroon, while the other four occur in the DRC; one of them (*M. bernice berenicides*) also occurs

in Rwanda, Burundi and Uganda. Although it has only been recorded from Ndola in our region, there is the possibility that it may be found in the upper reaches of the Zambezi.

Food plants: *Polygonum* spp.

4. *Eicochrysops hippocrates* Fabricius, 1793

White Tipped Blue

Diagnosis: The sooty ground colour and the prominent white tips of the forewings make the male a distinctive little butterfly. The female is very different, looking like a small *Euchrysops*, but the chalky underside with fine black markings is different from that genus and similar to that of the male.

Habitat & habits: Because of its host plants, which are almost wholly aquatic, this species is restricted to habitats with permanent water (swamps and river banks). It is a spring and summer butterfly. Males are perching species, usually sitting with the wings two-thirds open on the host plant, and they are extremely aggressive for their size. The flight is also rather rapid for such a delicate species. Both sexes visit flowers. Its illustrated life history is shown in Clark & Dickson (1971).

Conservation status: Not under any threat, but may be of use as an indicator of the health of the aquatic system.

Distribution: The species is found throughout most of Africa and Madagascar. Although widespread, this species tends to be localized within the Zambezi Basin, it is found from the origin of the Zambezi through to Victoria Falls. There are few records from Botswana, but it is not infrequent along the Chobe River from Serondella to Kazungula, though rarely in any numbers. It has not been seen in the hot and dry parts of the Zambezi below Victoria Falls to Chirundu.

Food plants: Larvae have been recorded on *Polygonum* and *Rumex* (Polygonaceae).

5. *Leptotes pulcher* (Murray), 1874

Beautiful Zebra Blue

Diagnosis: The upperside ground colour of the male of this small butterfly is a light and vivid violet; the female is also a lighter colour than the other *Leptotes*. The underside has more striking whitish marginal and submarginal markings than other members of the genus.

Habitat & habits: Almost exclusively tied to marshy habitats.

Conservation status: Although rare this species is not under any threat.

Distribution: There are records from most of Africa, though the species appears to be absent from many areas - widespread, local, but quite rare. Found intermittently at various localities along the entire length of the Zambezi, even in the hot parts such as Mlibizi and Deka. In Botswana it is chiefly found in the Okavango and Chobe river systems. Larsen (in prep.) states "where the Chobe river runs over stony ground between Kasane and Kazungula the species may be quite common, but it is usually not numerous". A spring and summer insect.

Food plants: Has been recorded on *Sesbania sesban* (Fabaceae: Papilionoideae).

6. *Cacyreus lingeus* (Stoll), 1782

Bush Bronze

Diagnosis: The upperside of this small butterfly is dark blue in the male and a lighter blue with white and brown in the female. The underside is a mosaic of white and brown.

Habitat & habits: Favourite habitat is the banks of streams through woodland. It has a weak fluttering flight and is often found settled on vegetation next to the river.

Conservation status: Not under any threat.

Distribution: Found throughout sub-Saharan Africa. Although its favourite habitat is along rivers in woodlands of various types, it is also found on the margins of forests. Within the Zambezi Basin it can be found in many places along the Zambezi and Chobe rivers where these pass through woodland.

Food plants: *Plectranthus*, *Salvia*, *Calamintha*, *Lavandula*, *Mentha* and *Hemizygia flabellifolia* (Lamiaceae).

7. *Cupidopsis cissus* (Godart), 1824

Common Meadow Blue

Diagnosis: A largish lycaenid, both sexes have rounded wings without tails. Male light blue, forewing with a narrow dark margin and apical area, hindwing anal angle with a red and black submarginal spot. The female is similar to the male but the blue areas are reduced and have several red and black hindwing submarginal spots. Underside is light grey with submarginal red markings and dark postdiscal spots.

Habitat & habits: Found in wet grasslands, grassy meadows and dambos; less often in woodlands. It is normally seen fluttering around flowers in the grass, although at times it flies quite rapidly just above them.

Conservation status: Not under any threat, but may be of use as an indicator of the health of grassland systems.

Distribution: Found throughout Africa and the Madagascar. There are indications that the West African, the South and East African and Madagascan populations may be subspecifically distinct. Along the length of the Zambezi this species is found in grasslands, but is probably rare in the middle sections.

Food plants: *Eriosema* sp., *Vigna* sp. Feeds on flowers and by burrowing into developing seeds; visited by ants.

8. *Zeretis fontainei* Stempffer, 1956

Fontain's Gem

9. *Zeretis sorhagenii* (Dewitz), 1879

Scarce Gem

Diagnosis: These two species are very distinctive, the underside being orange and black with numerous metallic silver-blue spots and the upperside is black-brown with orange spots. In *Z. sorhagenii* these orange spots are along the margin, while in *Z. fontainei* they are dispersed over the uppersurface.

Habitat & habits: Although these two species are not true swamp species, they are dambo-associated, very localized and rare. Within the region they have only been found in Mwinilunga District (the record of *Z. sorhagenii* from Kazungula by R.H.R. Stevenson in 1933 remains a mystery as it has not been seen there since). *Z. sorhagenii* was found in a small wet dambo a few hundred metres from the Zambezi River on Hillwood Farm. Similarly, *Z. fontainei* was found on a large wet dambo about 40 km SE of Mwinilunga. Both species fly little and remain in small colonies, often sitting on the ground or low vegetation.

Conservation status: Vulnerable.

Distribution: *Zeretis fontainei* has only been recorded from the DRC and NW Zambia. *Zeretis sorhagenii* also has a restricted distribution, having been found in Angola, southern DRC and in one locality in Mwinilunga District.

10. *Ypthimomorpha itonia* Hewitson, 1865

Swamp or Lesser Ringlet

Diagnosis: Apart from the eye-spots this species is uniformly brown above. There are usually 6 or 7 ocelli on the hindwing underside arranged in a straight line, some or all of which are also present on the upperside. These ocelli make it distinguishable from all its close relatives in the genus *Ypthima*, which have only 1 or 2 ocelli. Ocelli are sometimes reduced to tiny points during the dry season. The underside of the hindwings is crossed by two more or less distinct, straight brown discal bands, and the forewing eye-spot is usually oval in shape.

Habitat & habits: A smallish butterfly normally associated with moist environments such as swamps, marshes, bogs and permanent river margins. As long as the habitat is moist it matters little

whether the surroundings are arid, rainforest or semi-montane habitats. The flight is weak with a slight bobbing movement as it makes its way through the grass and swamp vegetation – a similar flight pattern to species of the genus *Ypthima*.

Conservation status: Not under any threat, and may be of use as an indicator of the health of the aquatic system.

Distribution: Found over most of Africa in savanna habitats, usually on somewhat swampy ground, but it does not go further south than N Botswana, Victoria Falls and E Zimbabwe. This species is likely to be found along the whole length of the Zambezi. In Botswana records are from Kazungula to Kasane, on the floodplain inside the main Chobe Forest, and in the northern Okavango.

11. *Acraea (Actinote) rahira rahira* Boisduval, 1833 Marsh Acraea

Diagnosis: The species can be recognized simply by the characteristic radial streaks at the margin of all four wings; the hindwing underside has no marginal lunules. The ground colour is lighter than that of the upperside, but the black discal spots are usually interconnected by orange streaks; there are also orange marginal streaks.

Habitat & habits: The habitat is always a marshy place (including the edges of dams) or floodplain. It may sometimes be extremely numerous. Flight is low down and very weak, not wandering very far from its food plant. The species is greatly attracted to the flowers of *Polygonum*, on which it often perches. The lifecycle is illustrated in van Son (1963).

Conservation status: Not under any threat, and may be of use as an indicator of the health of the aquatic system.

Distribution: Restricted to marshy habitats in southern, eastern and central Africa (N Botswana, Zimbabwe and Namibia to Kenya and Uganda). There are three subspecies, one in S Tanzania, one in W Kenya and Uganda, and the nominate one covering the rest of its distribution. It occurs along most of the Zambezi wherever its larval food plant occurs, and in the swampy parts of the Chobe/Linyanti system.

Food plants: *Persicaria attenuata* (formerly *Polygonum pulchrum*) and *Conyza canadensis* (= *Erigeron canadense*).

12. *Acraea ventura ventura* Hewitson, 1877 Banded Orange Acraea

Diagnosis: A small to medium orange species, with black borders on both fore and hindwings enclosing orange spots along the margins. The black submarginal bar is always fully formed from the costa to outer margin isolating the orange apical area on the forewing. The hindwing underside has orange submarginal and discal markings. The female is similar but with a large dark apical area enclosing a whitish band.

Habitat & habits: Most often found in marshy grassland, and wide ranging. It has having a slow floating flight except when disturbed, when it flies with a rapid and slightly zig-zag movement.

Conservation status: Not under any threat.

Distribution: The nominate subspecies is widespread in the northern part of Zambia, Shaba Province of DRC through to Malawi and S Tanzania. *A. v. ochrascens* occurs in Kivu Province of the DRC, Rwanda, Burundi, NW Tanzania, Uganda and W Kenya, although some authors regard it as form *ochrascens*. It is found in the first section of the Zambezi, and although not recorded from the Lower Shire marshes it may occur here as it has been recorded from swamps near Mt Mulanje.

Food plants: Possibly *Senna* species.

13. *Acraea mirifica* Lathy, 1906 Dark Marsh Acraea

Diagnosis: The male of this species is unmistakable with the upperside being dark brown to black with a broad yellowish-white subapical band. The hindwing has a few yellow submarginal spots,

while the underside is cream with black spots arranged in the normal acraea pattern. The female is unlike the male and is mid-brown with a dark border to both wings and an apical patch on the forewing.

Habitat & habits: Found in marshy vegetation adjoining streams. The males do not venture away from their marshy habitat and sit on grass stems awaiting the approach of females.

Conservation status: Vulnerable.

Distribution: Northern part of Zambia, Bihe District of Angola, and the Shaba and Lualaba districts of the DRC. This rare, localized species is found in marshy areas next to streams in upper parts of the Zambezi. There is a colony in a small marsh along the Sakeji River on Hillwood Farm, the first tributary of the Zambezi.

14. *Acraea acerata* Hewitson, 1874

The Falls Acraea

Diagnosis: The upperside of this small butterfly is yellow-orange with broad black margins. There is a black submarginal bar from the costa to the outer margin isolating the yellow-orange apical area on the forewing. The yellow on the forewing does not intrude into the cell. The hindwing has one or two spots in the discal area near the costa.

Habitat & habits: Normally found near water. It is a weak flier and tends to prefer vegetated areas near marshes.

Conservation status: Not under any threat.

Distribution: Found sporadically over most of the Afrotropical Region north of the Zambezi and Cunene. Although the species is usually found near water, in certain areas it has moved into cultivated patches near rivers or in very wet areas, where it can be a pest on sweet potatoes. Occurs in Barotseland through to Victoria Falls and along the Chobe River at Shakawe and Kasane. It probably also occurs along the Lower Shire and has also been recorded from Blantyre and Mulanje.

Food plants: *Solanum*, *Ipomoea*, *Lepistemon*, *Merremia*, *Vernonia*, *Passiflora* and *Zea* (van Someren & Rogers 1926).

15. *Acraea periphanes* Oberthur, 1893

(no common name)

Diagnosis: A medium sized polymorphic species. The ground colour is light orange-brown, both wings have numerous spots, forewing with or without black apical patch, and veins darkened towards the apex margins. The female is similar but usually duller brown, sometimes greyish-brown with a light area at the distal half of the forewing.

Habitat & habits: Found in marshy grassland. It is a fairly strong flier.

Conservation status: ?Vulnerable.

Distribution: Within its habitat it is found in Angola, N Zambia, N Malawi, S and W Tanzania and the DRC (Haut-Lomani, Lualaba and Haut-Shaba provinces). In the Zambezi Basin it is restricted to the northern part of Zambia and the adjoining area of Angola.

16. *Catacroptera cloanthe* (Stoll), 1781

Pirate

Although this is a widespread and common species, it is included here as it is often found along stream banks and in marshy areas.

Diagnosis: The species is orange-brown with dark brown spots and bars on the forewing and a submarginal row of blue centred eyespots on the hindwing. Unusual features of this butterfly are the tufts of cilia at the ends of the veins at the margins of both wings, and the hairy body and wing underside. The sexes are similar.

Habitat & habits: Although preferring marshy areas and stream banks, it can be found in most grassy landscapes. Specimens are usually encountered singly and are wary, normally gliding away quickly when approached. Description of the early stages is given in van Son (1979).

Conservation status: Not under any threat.

Distribution: Found throughout sub-Saharan Africa, with subspecies *C. cloanthe ligata* from Senegal to Cameroon and the nominate subspecies through the rest of Africa. Found along the whole length of the Zambezi.

Food plants: *Justicia protracta*, *Ruellia cordata* and *Asclepias* spp.

17. *Junonia ceryne ceryne* (De Boisduval), 1847 Marsh Commodore

Diagnosis: One of the smaller *Junonia*. Ground colour is brown with a broad pale red-brown median band across both wings which is paler proximally. The dry season form *tukuoa* has more angular wings and the forewing is more falcate. Sexes are similar.

Habitat & habits: Locally common in marshes along streams and rivers. It flies slowly, but can put on considerable speed when disturbed, frequently settling on low vegetation or the ground with their wings open. The life history is given by van Son (1979).

Conservation status: Not under any threat.

Distribution: The nominate subspecies occurs from the Transkei up the Indian Ocean coast to Kenya, from Zimbabwe to Angola and across the DRC to Uganda, Kenya and Ethiopia. The second subspecies, *J. c. ceruana*, occurs in Cameroon, Nigeria and Guinea. Found in the upper Zambezi, the Lower Shire marshes and the delta.

Food plants: *Pycnostachys reticulata*, *Plectranthus* sp., *Scabiosa* sp., *Coleus* sp. and *Plastostema* sp.

18. *Neptis jordani* Neave, 1910 Jordan's Sailer

Diagnosis: All *Neptis* have a characteristic black and white appearance. This small, distinctive species has its forewing submarginal lines in areas 3, 4 and 6 clearly interrupted by dark veins and the white band narrows towards the costa, giving the outer edge a kink. The sexes are similar.

Habitat & habits: The species shows a preference for riverine and grassy marshes. Its flight is low and comparatively slow, and it frequently settles on low-growing vegetation close to the edge of the water.

Conservation status: Not under any threat.

Distribution: Found from N Botswana to Zambia, DRC, Rwanda, Burundi, Tanzania, Malawi, Mozambique and E Zimbabwe. Recorded from the upper reaches of the Zambezi and along the Chobe River. It is probably absent from the Middle Zambezi but reoccurs in the Lower Shire and Zambezi Delta.

19. *Pseudargynnis hegemone* (Godart), 1819 False Fritillary

Diagnosis: A medium sized butterfly, orange with numerous black spots. Similar to *Phalantha phalanta*, but it can be distinguished by the more rounded wings and different arrangement of spots. Sexes are similar. Seasonally variable, the wet season form differs from the dry season form *nyassae* in the heavier black spotting.

Habitat & habits: The species is not so tied to marshy areas as others listed here, and is found in both marshes and open glades on forest edges. It flies with a gliding motion just above the vegetation, settling often with its wings open.

Conservation status: Not under any threat.

Distribution: Found in marshy areas from Cameroon to Angola and eastwards to Zambia, Malawi, W Tanzania, W Kenya and S Sudan. Found in the Zambezi headwaters and, although not recorded from the Lower Shire, it may occur here as there are records from Cholo and Mt Mulanje. A single 1934 record from Lomagundi in Zimbabwe has never been substantiated and is probably erroneous.

20. *Parnara monasi* (Trimen), 1889

Water Watchman

Diagnosis: This little butterfly looks much like a *Borbo* but the antennae are noticeably shorter. There is a single spot in the forewing cell, while the hindwing has a row of regularly placed white spots on both the upper and the under surfaces. The spots on the hindwing underside are often framed with dark scales. The male differs from most *Borbo* in lacking the spot in space 1b, but it is present in the female.

Habitat & habits: As the common name implies, this species is associated with water, flying in grass along rivers and lakes and occasionally on the edge of bush. Illustrated life history is given in Pennington (1978).

Conservation status: Not under any threat.

Distribution: Found over most of Africa, but is not particularly common. It seems to be missing from large areas which seem superficially suitable. Although widespread, it is not common along the Zambezi and has only been recorded from Mongu, the Shire lowlands and the Zambezi Delta. In Botswana it is essentially linked to the Okavango and Chobe river systems.

Food plants: *Saccharum* and various riverine grasses.

21. *Borbo micans* (Holland), 1896

Marsh Swift

Diagnosis: The upperside of the male has a distinctive orange-brown colouring with ochrous spots. The underside is similar but slightly lighter in colour. The female is similar in colour but is quite distinctly spotted (large hyaline spots on forewing with a non-hyaline discal spot near the inner margin).

Habitat & habits: An inhabitant of marshes, swamps and marshy areas along rivers. In these habitats it flies low and relatively slowly over the grass, often settling on conspicuous blades. The males establish relatively small territories (5-10 m²) where they perch on blades of grass from which they dart out and chase off intruders. The females seem to fly at random in the swampy area, presumably searching for suitable food plants.

Conservation status: Not under any threat.

Distribution: Found throughout sub-Saharan Africa (in South Africa only one specimen has been taken near Kosi Bay). So far it has been recorded only from the upper section of the Zambezi and the Chobe/Linyanti system. It is likely to occur from the source through to Barotseland, and may even occur around Kazungula. It should then reoccur somewhere near Nhamilabue and go through to the Zambezi Delta.

Food plants: Possibly swamp grasses (Poaceae).

10.6 DISCUSSION

10.6.1 Butterfly faunas

The area around the source of the Zambezi and the surrounding river systems is rich in butterfly and emperor moth species (Table 10.3). Approximately half of Zambia's total butterfly species can be found in this area. Of the 21 wetland species listed, 18 are found in Mwinilunga District, and probably also the remaining three. The first section of the Zambezi contains species which are distributed from south central Angola through the Shaba Province of the DRC and over much of Zambia, excluding the drier parts of the Zambezi Valley. This faunal assemblage is known as Zambesian following Carcasson (1964). Typical or characteristic species include *Graphium taboranus*, *Belenois rubrosignata*, *Bicyclus cottrelli*, *B. cooksoni*, *Neocoenyra cooksoni*, *Physcaeneura pione*, *Charaxes bohemani*, *C. guderiana*, *C. penricei*, *C. fulgurata*, *Euriphene iris*, *Pseudacraea poggei*, *Neptis jordani*, *Junonia touhilimasa*, *J. artaxia*, *J. actia*, *Acraea guillemei*, *A. asema*, *A. omrora*, *A. mansya*, *A. periphanes*, *A. chaeribula*, *A. mirifica*, *Liptena homeyeri*, *L.*

eukrines, *Deloneura subfusca*, *Deudorix kafuensis*, *Iolaus australis*, *Iolaus violacea*, *Lepidochrysops pampolis*, *Euchrysops katangae*, *Sarangesa astrigera*, *S. pandaensis*, *Abantis zambesiaca*, *Metisella kambove*, *M. angolana*, *Teniorhinus harona*, *Meza larea*, *Fresna nyassae* and *Brusa saxicola*. Many of these species are absent from the other sections of the Zambezi (Table 10.1).

Although there is little material from Barotseland, the small amount of collecting that has taken place suggests this section has affinities with both the Zambesian and Kalahari faunas, but possibly more with the former. Species linking it with this zone are *Sallya benguelae*, *Charaxes guderiana* and *Neptis jordani*, while *Acraea atolmis* and *A. atergatis* link it with the Kalahari zone. Most of the species so far collected are eclectic (widespread) species, suggesting incomplete collecting. In addition to the five true wetland and swamp species listed, a further eight should be present (*Leptosia alcesta*, *Acraea rahira*, *Junonia ceryne*, *Ypthimomorpha itonia*, *Cacyreus lineus*, *Cupidopsis cissus*, *Eicochrysops hippocrates* and *Parnara monasi*). It is estimated that the number of species would increase at least four-fold if further collecting in swamps and woodlands was carried out.

The next section, from Senanga to Victoria Falls, include species more typical of the Kalahari system, but still contains elements from the Zambesian region such as *Neptis jordani* and *Charaxes fulgurata*. Similarly the Chobe/Linyanti system, although having strong affinities with the Kalahari, also has affinities with the Zambesian region. An indication of this is the presence of species such as *Charaxes bohemani*, *C. guderiana* and *Neptis jordani*. Species characteristic of the Kalahari region are *Charaxes phaeus*, *C. zoolina*, *Graphium porthaon*, *Colotis agoie*, *C. amatus calais*, *C. celimene amina*, *C. danae annae*, *C. evenina evenina*, *C. ione*, *C. pallene*, *Aloeides damarensis*, *A. molomo*, *Anthene amarah*, *Azanus jesous*, *A. moriqua*, *Crudaria leroma*, *Epamera mimosae rhodosense*, *Iolaus bowkeri tearei*, *Lepidochrysops plebeia*, *Spindasis phanes*, *Zintha hintza hintza*, *Gegenes pumilio*, *Sarangesa seineri* and *Spialia delagoae*. Of the 20 wetland species listed in the review, nine have been recorded from the Chobe/Linyanti area, and it is likely that a few additional wetland species such as *Catacroptera cloanthe* will also be found.

The fourth section of the Zambezi is more typical of the drier Kalahari zone, which includes parts of Matabeleland, the former northern Transvaal, the northeastern Cape, Botswana, the western half of Namibia and southern Angola. In addition to the species mentioned above, other species characteristic of this zone that occur in this section are *Charaxes vansoni*, *Colotis vesta mutans*, *Dixeia doxo parva*, *Nepheronia buquetii buquetii*, *Lepidochrysops glauca* and *Bicyclus ena*. The genus *Colotis* is well represented in this section with 13 species having been recorded, followed by Section 3 with 11 species. The high number of *Colotis* species in this section is an indication of its adaptation to hotter and drier conditions. The more eastern part of this section is wetter, as shown by species such as *Charaxes cithaeron joanae*, *Euphaedra neophron neophron* and *Euriphene iris*.

On entering the Lower Shire a few of the more wet-adapted species, such as *Charaxes pollux geminus*, *Euphaedra neophron neophron* and *Neptis jordani*, are seen. This region, apart from having swamp-adapted species, shows affinities with the Kalahari and Zambesian zones. Although only six wetland species have been recorded, it is likely that a further eight will be found (*Mylothris rubricosta*, *Acraea rahira*, *A. acerata*, *Ypthimomorpha itonia*, *Cupidopsis cissus*, *Eicochrysops hippocrates*, *Leptotes pulcher* and *Borbo micans*).

Due to the paucity of records from the area below the Shire, little can be said about Section 6. It is likely that the portion from the Shire to the Zambezi Delta will contain species characteristic of the lowland eastern woodland and forests such as *Appias lasti*, *Euxanthe wakefieldi*, *Charaxes violetta*,

C. lasti, *Euryphura achlys*, *Neptis goochi*, *Hypolimnas deceptor*, *Acraea rabbaiae*, *A. satis*, *Pentila tropicalis*, *Argiolaus lalos*, *Axiocerces punicea*, *Anthene lasti* and *Gorgyra subflavida*. In the area around the delta, coastal species such as *Colotis eunoma*, which appears to be restricted to littoral sand dunes, may be found, along with many of the common dry-adapted species.

Table 10.3 Number of butterfly and emperor moth species (not including subspecies) for the six faunal sections of the Zambezi River, including those possibly in Section 5.

Family/subfamily	Section of Zambezi						Total
	1	2	3	4	5	6	
Nymphalidae							
Acraeinae	42	6	14	12	3	3	54
Charaxinae	32	3	13	15	7	0	41
Argynninae	3	1	1	1	2	0	3
Danainae	6	1	1	1	2	2	7
Libytheinae	0	0	0	1	1	0	1
Limenitinae	62	7	10	9	8	0	66
Nymphalinae	26	8	12	14	15	13	26
Satyrinae	33	4	10	11	11	3	41
Riodinidae	1	0	0	0	0	0	1
Papilionidae	16	4	10	5	7	3	19
Pieridae	35	13	25	31	26	6	47
Lycaenidae	103	7	53	33	30	9	155
Hesperiidae							
Coeliadinae	3	0	2	1	1	0	3
Hesperiinae	80	3	16	11	8	4	87
Pyrginae	25	1	14	9	4	1	37
Total butterflies	467	58	181	154	125	44	588
Saturnidae (emperor moths)	57	36	38	45	42	3	63

Along the length of the Zambezi there are also many butterfly species that are particularly adaptable (eclectic species). These are able to establish themselves in a great variety of habitats throughout Africa. Most are species of open formations and occur almost everywhere except on the higher mountains and under extreme desert conditions. Their presence within forests is usually due to their ability to colonize such man-made habitats as road edges, footpaths, clearings, plantations and gardens. These adaptable species include *Papilio demodocus*, *Belenois gidica*, *B. creona*, *B. aurota*,

Mylothris agathina, *Catopsilia florella*, *Eurema hecabe*, *E. brigitta*, *E. desjardinsii*, *Danaus chrysippus*, *Hamanumida daedalus*, *Neptis saclava*, *Byblia anvatarata*, *Byblia ilithyia*, *Eurytela dryope*, *Hypolimnna misippus*, *Junonia oenone*, *J. hierta*, *Jorithya*, *Cynthia cardui*, *Acraea encedon*, *A. eponina*, *Deudorix antalus*, *Anthene definita*, *Lampides boeticus*, *Zizula hylax*, *Zizeeria knysna*, *Coeliades forestan*, *Tagiades flesus* and *Peliopidas mathias*.

The Zambezi passes through four broad faunal regions – the Zambesian, Kalahari, Eastern Woodland and Coastal – and is therefore rich in butterfly diversity. This diversity is particularly noticeable when one considers the higher taxonomic categories. For example, certain genera found on the western side of the rift, such as *Liptena*, *Epitola*, *Oxylides* and *Telipna*, are not present or scarce in the east. Genera with their centres of origin in East or Southern Africa, such as the lycaenid genera *Capys* and *Cnodontes*, are either absent or rare in the western forests. The Zambezi Basin, has genera from both the western and eastern regions with 146 genera having been recorded from along the river itself.

The Zambezi Valley may also act as a barrier to butterfly movement. Some species found just north of the valley are not present in the south, for instance *Belenois crawshayi*. Many of these species are associated with miombo woodland and are probably unable to move across the hot, low-lying Zambezi Valley.

10.6.2 Conservation

The major concern for conservation is the small riverine forests to the west of Kalene Hill in the extreme northwest of Zambia. These forests provide the habitat and food plants for many of the unusual species recorded from this area, it is important to have an on-the-ground assessment so that the present state of the forest patches is truly known. Once an area of rainforest has been laid bare, its immense ecological complexity is unlikely to regenerate within historical time.

Most wetland butterfly species are closely linked to wetlands and would not be able to survive without them, with the possible exception of *Cacyreus lingeus*, *Leptosia alcesta*, *Cupidopsis cissus*, *Ypthimomorpha itonia* and *Catacroptera cloanthe* which can survive in drier habitats. Wetland species of particular interest are *Acraea periphanes*, *A. mirifica*, *Mylothris rubricosta*, *Zeritis fontainei* and *Z. sorhagenii*. The others are widely distributed in Africa and are not under any threat on a continental basis. All five species of interest have been recorded from the first section of the Zambezi; the only one recorded from other sections (2 and 3) is *M. rubricosta* which has a wider distribution than the others but is rather localized. Of these five species, *Zeritis fontainei* and *Acraea mirifica* have the most restricted total distributions, and the Zambezi Basin holds an important proportion of the global population. These two species are the most threatened, either due to habitat destruction or drying-out of their habitats.

10.7 CONCLUSIONS

The Mwinilunga area of the Zambezi is the most important area within the basin for butterfly diversity. This applies to both wetland and riparian species. In addition, two wetland species considered to be under global threat occur in this section. The Zambezi from Victoria Falls through to Tete has a distinctive fauna consisting of the more dry-adapted species, but none are under threat.

It is clear, from the paucity of records, that further research is required in the Barotseland area and in the Zambezi Delta. Although only 58 species are listed here for Barotseland, the presence of

Erikssonina acraeina suggests other species of interest may be present and many more could be added to this list. Further research in the Barotseland area is required to confirm and assess the affinities and importance of this section compared to the others. The present information suggests it forms a strong link between the wet Zambesian zone and the drier Kalahari zone, with a possible predominance of the Zambesian elements. With further collecting it is likely that this section would rank as the second most diverse part of the Zambezi.

It is probable that the low number of species from the Lower Shire is due to inadequate sampling, but the number of species is still expected to be lower than for Barotseland. It appears to form a link between the drier Kalahari, wetter Zambesian and eastern forest or woodland zones. Unfortunately, conclusions cannot be drawn for the Zambezi Delta. It should contain many elements from the East African woodlands and coastal zones, and some of the rare coastal species are expected to occur.

10.8 REFERENCES

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Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
<i>Charaxes howarthi</i> Minig, 1976		X								
<i>Charaxes imperialis lisomboensis</i> van Someren, 1975		X								
<i>Charaxes jahlusa argynnides</i> Westwood, 1864								X		
<i>Charaxes jahlusa rex</i> Henning, 1978								X		
<i>Charaxes jasius saturnus</i> Butler, 1865		X		X	X	X	X	X	X	X
<i>Charaxes like catachrous</i> van Someren & Jackson, 1952		X								
<i>Charaxes lucretius intermedius</i> van Someren, 1971		X								
<i>Charaxes lucretius schofieldi</i> Plantrou, 1989		X								
<i>Charaxes manica</i> Trimen, 1894								X		
<i>Charaxes nichetes pantherinus</i> Rousseau-Decelle, 1934		X								
<i>Charaxes numenes aequatorialis</i> van Someren, 1972		X								
<i>Charaxes penricei penricei</i> Rothschild, 1900		X			X					
<i>Charaxes phaeus</i> Hewitson, 1877				X		X		X		
<i>Charaxes pollux geminus</i> Rothschild, 1900									X	X
<i>Charaxes pollux pollux</i> (Cramer), 1775		X								
<i>Charaxes protoclea azota</i> (Hewitson), 1877		X								
<i>Charaxes protoclea catenaria</i> Rousseau-Decelle, 1934		X								
<i>Charaxes pythodoris pythodoris</i> Hewitson, 1873		X								
<i>Charaxes vansoni</i> van Someren, 1975						X				
<i>Charaxes varanes vologeses</i> (Mabille), 1876		X	X	X	X	X	X	X	X	X
<i>Charaxes variata</i> van Someren, 1969		X								
<i>Charaxes zoolina zoolina</i> (Westwood), 1850				X	X	X		X	P	
<i>Euxanthe crossleyi crossleyi</i> (Ward), 1871		X								
<i>Euxanthe wakefieldi</i> (Ward), 1873								X		
Argynninae										
<i>Lachnoptera anticlia</i> (Hubner), 1819		X								
<i>Phalanta eurytis eurytis</i> (Doubleday), 1847		X							P	
<i>Phalanta phalantha aethiopica</i> (Rothschild & Jordan), 1903		X	X	X	X	X	X	X	X	X
Danainae										
<i>Amauris (Amaura) damocles hyalites</i> Butler, 1874		X								
<i>Amauris (Amaura) dannfelti restricta</i> Talbot, 1940		X								
<i>Amauris (Amauris) niavius niavius</i> (Linnaeus), 1758		X								
<i>Amauris (Amauris) ochlea ochlea</i> (Boisduval), 1847									P	X
<i>Amauris (Amauris) tartarea tartarea</i> Mabille, 1876		X								
<i>Danaus (Anosia) chrysippus aegyptius</i> (Schreber), 1759		X	X	X	X	X	X	X	X	X
<i>Tirumala petiverana</i> (Doubleday), 1847		X								
Libytheinae										
<i>Libythea labdaca laius</i> Trimen, 1879								X	P	
Limenitinae										
<i>Aterica galene galene</i> (Brown), 1776		X								X
<i>Bebearia aurora theia</i> Hecq, 1989		X								
<i>Bebearia orientis orientis</i> (Karsch), 1895								X		X
<i>Bebearia plistonax</i> (Hewitson), 1874		X								
<i>Bebearia schoutedeni</i> (Overlaet), 1954		X								
<i>Bebearia senegalensis katera</i> (van Someren), 1939		X								
<i>Byblia anvatara acheloia</i> (Wallengren), 1857		X		X	X		X	X	X	X
<i>Byblia ilithyia</i> (Drury), 1773			X	X	X					

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
<i>Bicyclus mesogena mesogena</i> (Karsch), 1894		X								
<i>Bicyclus moyses</i> Condamin & Fox, 1964		X								
<i>Bicyclus safitza safitza</i> (Westwood), 1850		X							X	X
<i>Bicyclus sandace</i> (Hewitson), 1877		X								
<i>Bicyclus sebetus</i> (Hewitson), 1877		X								
<i>Bicyclus sophrosyne overlaeti</i> Condamin, 1965		X								
<i>Bicyclus suffusa suffusa</i> (Riley), 1921		X								
<i>Bicyclus trilophus trilophus</i> (Rebel), 1914		X								
<i>Bicyclus vansoni</i> Condamin, 1965		X								
<i>Bicyclus vulgaris</i> (Butler), 1869		X								
<i>Coenyropsis bera</i> (Hewitson), 1877		X					X		X	X
<i>Gnophodes betsimena parmeno</i> Doubleday, 1849		X								
<i>Henotesia centralis</i> Aurivillius, 1903		X								
<i>Henotesia perspicua</i> (Trimen), 1873									X	X
<i>Henotesia phaea katangensis</i> Overlaet, 1955		X								
<i>Henotesia simonsii</i> (Butler), 1877				X	X	X	X		X	X
<i>Henotesia teratia</i> (Karsch), 1894		X								
<i>Melanitis leda helena</i> (Westwood), 1851		X	X	X	X	X	X	X	X	X
<i>Melanitis libya</i> Distant, 1882		X						X		
<i>Neocoenyra cooksoni</i> Druce, 1907		X								
<i>Physcaeneura pione</i> Godman, 1880		X						X	X	X
<i>Ypthima antennata antennata</i> van Son, 1955					X		X		X	X
<i>Ypthima asterope asterope</i> (Klug), 1832						X			X	X
<i>Ypthima condamini condamini</i> Kielland, 1982									X	X
<i>Ypthima congoana</i> Overlaet, 1955		X								
<i>Ypthima diplommata</i> Overlaet, 1954		X	X							
<i>Ypthima granulosa</i> Butler, 1883				X	X	X				
<i>Ypthima impura paupera</i> Ungemach, 1932		X	X							
<i>Ypthima praestans</i> Overlaet, 1954		X			X					
<i>Ypthima pulchra</i> Overlaet, 1954		X								
<i>Ypthima pupillaris pupillaris</i> Butler, 1888		X								
<i>Ypthima recta</i> Overlaet, 1955		X								
<i>Ypthima rhodesiana</i> Carcasson, 1961							X	X		
<i>Ypthimomorpha itonia</i> (Hewitson), 1865	●	X		X	X	X				X
RIODINIDAE										
<i>Abisara rogersi dollmani</i> Riley, 1932		X								
PAPILIONIDAE										
<i>Graphium adamastor</i> (Boisduval), 1836		X								
<i>Graphium almansor almansor</i> (Honrath), 1884		X								
<i>Graphium angolanus angolanus</i> (Goeze), 1779		X	X	X	X	X			X	X
<i>Graphium antheus</i> (Cramer), 1779		X	X	X	X	X	X	X	X	X
<i>Graphium leonidas leonidas</i> (Fabricius), 1793		X	X	X	X	X	X	X	X	X
<i>Graphium poggianus poggianus</i> (Honrath), 1884		X								
<i>Graphium polícenes polícenes</i> (Cramer), 1775		X								
<i>Graphium porthaon porthaon</i> (Hewitson), 1865				X	X	X		X	P	

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
<i>Aphnaeus erikssoni</i> Trimen, 1891		X								
<i>Argyroshela inundifera</i> Hawker-Smith, 1933		X								
<i>Aslauga marshalli</i> ? Butler, 1899		X								
<i>Aslauga purpurascens</i> Holland, 1890		X								
<i>Aslauga vininga</i> (Hewitson), 1875		X								
<i>Axiocerses amanga</i> (Westwood), 1881				X		X		X	X	X
<i>Axiocerses bambana</i> Grose-Smith, 1900									X	X
<i>Axiocerses tjoane</i> (Wallengren), 1857				X	X	X		X		
<i>Axiocerses tjoane rubescens</i> Henning & Henning, 1996		X								
<i>Azonus isis</i> (Drury), 1773		X								
<i>Azonus jesous jesous</i> (Guerin-Meneville), 1849				X		X				
<i>Azonus mirza</i> (Plotz), 1880		X								
<i>Azonus moriqua</i> (Wallengren), 1857				X		X				
<i>Azonus natalensis</i> (Trimen), 1887							X			X
<i>Azonus ubaldus</i> (Stoll), 1782						X				
<i>Baliochila hildegarda</i> (Kirby), 1887		X								
<i>Cacyreus lingeus</i> (Stoll), 1782		● X							X	X
<i>Cacyreus marshalli</i> Butler, 1898				X						
<i>Cacyreus virilis</i> Aurivillius, 1924				X					P	
<i>Citrinophila terias</i> Joicey & Talbot, 1921		X								
<i>Cnodontes pallida</i> (Trimen), 1898								X		
<i>Cnodontes vansomereni</i> Stempffer & Bennett, 1953								X		
<i>Crudaria leroma</i> (Wallengren), 1857				X	X	X				
<i>Cupidesthes arescopia orientalis</i> (Stempffer), 1962		X								
<i>Cupidopsis cissus</i> (Godart), 1824		● X		X						
<i>Cupidopsis jobates jobates</i> (Hopffer), 1855				X		X				
<i>Deloneura subfusca</i> Hawker-Smith, 1933		X								
<i>Deudorix (Actis) mimeta mimeta</i> (Karsch), 1895		X								
<i>Deudorix (Hypokopelates) kafuensis</i> Neave, 1910		X								
<i>Deudorix (Pilodeudorix) caerulea</i> Druce, 1890							X			
<i>Deudorix (Pilodeudorix) zeloides</i> (Butler), 1901		X								
<i>Deudorix (Virachola) antalus</i> (Hopffer), 1855			X	X		X	X	X	X	X
<i>Deudorix (Virachola) dinochares</i> Grose-Smith, 1887				X	X		X	X		
<i>Deudorix (Virachola) diocles</i> Hewitson, 1869							X		X	
<i>Deudorix (Virachola) jacksoni</i> Talbot, 1935		X								
<i>Deudorix (Virachola) lorisona coffea</i> Jackson, 1966					X					
<i>Eicochrysops hippocrates</i> (Fabricius), 1793		● X	X	X	X	X				X
<i>Eicochrysops messapus mahallakoena</i> (Wallengren), 1857		X		X		X				
<i>Eicochrysops pinheyi</i> Heath, 1985		X								
<i>Epitola carcina</i> Hewitson, 1873		X								
<i>Epitola</i> sp.		X								
<i>Epitola katerae</i> Jackson, 1962		X								
<i>Epitola mpangensis</i> Jackson, 1962		X								
<i>Epitola subgriseata</i> ? Jackson, 1964		X								
<i>Epitola viridana viridana</i> Joicey & Talbot, 1921		X								
<i>Eresina toroensis</i> Joicey & Talbot, 1921		X								
<i>Erikssonia acraeina</i> Trimen, 1891			X							

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
<i>Liptena praestans congoensis</i> Schultze, 1923		X								
<i>Liptena xanthostola xantha</i> (Grose-Smith), 1901		X								
<i>Mimacraea marshalli marshalli</i> Trimen, 1898		X								
<i>Mimacraea skoptoles</i> Druce, 1907		X								
<i>Myrina silenus silenus</i> (Fabricius), 1775		X								
<i>Neurellipes gemmifera</i> (Neave), 1910		X								
<i>Oboronia guessfeldti</i> (Dewitz), 1879		X								
<i>Ornipholidotos overlaeti</i> Stempffer, 1947		X								
<i>Ornipholidotos peucetia peucetia</i> (Hewitson), 1866		X								
<i>Oxylides faunus albata</i> (Aurivillius), 1895		X								
<i>Pentila inconspicua?</i> Druce, 1910		X								
<i>Pentila pauli elisabetha</i> Hulstaert, 1924		X								
<i>Pentila pauli nyassana</i> Aurivillius, 1898									X	X
<i>Pentila pauli obsoleta</i> Hawker-Smith, 1933					X					
<i>Pentila tropicalis tropicalis</i> (Boisduval), 1847					X					
<i>Pentila umangiana meridionalis</i> Berger, 1981		X								
<i>Phlyaria heritsia virgo</i> (Butler), 1896		X								
<i>Pseudonacaduba aethiops</i> (Mabille), 1877		X								
<i>Pseudonacaduba sichela sichela</i> (Wallengren), 1857		X							P	
<i>Spalgis lemolea</i> Druce, 1890					X					
<i>Spindasis brunnea</i> Jackson, 1966					X					
<i>Spindasis ella</i> (Hewitson), 1865				X		X	X	X		
<i>Spindasis homeyeri</i> (Dewitz), 1887		X								
<i>Spindasis modestus heathi</i> D'Abbrera, 1980		X								
<i>Spindasis mozambica</i> (Bertolini), 1850		X								
<i>Spindasis natalensis</i> (Westwood), 1851				X	X	X			P	
<i>Spindasis phanes</i> (Trimen), 1873				X	X			X		
<i>Tarucus sybaris sybaris</i> (Hopffer), 1855				X		X				
<i>Telipna ruspinoidea katangae</i> Stempffer, 1961		X								
<i>Teratoneura isabellae congoensis</i> Stempffer, 1954		X								
<i>Thermoniphas distincta</i> (Talbot), 1935		X								
<i>Thermoniphas fontainei</i> Stempffer, 1956		X								
<i>Thermoniphas micyclus colorata</i> (Ungemach), 1932		X			X					
<i>Triclema nigeriae</i> (Aurivillius), 1905		X								
<i>Tuxentius calice calice</i> (Hopffer), 1855		X		X				X		
<i>Tuxentius melaena melaena</i> (Trimen), 1887		X		X					P	
<i>Uranothauma antinorii felthami</i> (Stevenson), 1934		X								
<i>Uranothauma falkensteini</i> (Dewitz), 1879		X								
<i>Uranothauma poggei</i> (Dewitz), 1879		X								
<i>Zeritis fontainei</i> Stempffer, 1956	●	X								
<i>Zeritis sorhagenii</i> (Dewitz), 1879	●	X								
<i>Zintha hintza hintza</i> (Trimen), 1864				X	X	X				
<i>Zizeeria knysna</i> (Trimen), 1862				X		X		X		X
<i>Zizula hylax</i> (Fabricius), 1775				X	X	X		X	X	X

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
<i>Zophopetes dysmephila</i> (Trimen), 1868				X						
Pyrginae										
<i>Abantis bamptoni</i> Collins & Larsen, 1994		X								
<i>Abantis contigua</i> Evans, 1937		X								
<i>Abantis paradisea</i> (Butler), 1870				X					P	
<i>Abantis venosa</i> , Trimen, 1889		X					X	X		
<i>Abantis vidua</i> Weymer, 1901		X								
<i>Abantis zambesiaca</i> (Westwood), 1874		X							X	X
<i>Calleagris hollandi</i> (Butler), 1897		X								
<i>Calleagris jamesoni jamesoni</i> (Sharpe), 1890		X		X						
<i>Calleagris lacteus</i> (Mabille), 1877		X								
<i>Caprona pillaana</i> Wallengren, 1857				X		X				
<i>Celaenorrhinus bettoni</i> Butler, 1902		X								
<i>Celaenorrhinus galenus</i> (Fabricius), 1793		X								
<i>Eagris decastigma</i> Mabille, 1891		X								
<i>Eagris lucetia</i> (Hewitson), 1875		X								
<i>Eretis melania</i> Mabille, 1891		X								
<i>Gomalia elma elma</i> (Trimen), 1862				X		X		X		
<i>Katreus hollandi</i> (Druce), 1909		X								
<i>Katreus holocausta</i> (Mabille), 1891		X								
<i>Leucochitonea levubu</i> Wallengren, 1857					X	X		X		
<i>Netrobalane canopus</i> (Trimen), 1864		X								
<i>Sarangesa astrigera</i>		X								
<i>Sarangesa brigida brigida</i> (Plotz), 1879		X								
<i>Sarangesa laelius</i> (Mabille), 1877		X								
<i>Sarangesa lucidella lucidella</i> (Mabille), 1891				X	X		X			
<i>Sarangesa maculata</i> (Mabille), 1891		X								
<i>Sarangesa motozi</i> (Wallengren), 1857					X					
<i>Sarangesa pandaensis deningi</i> Evans, 1956		X								
<i>Sarangesa phidyle</i> (Walker), 1870				X	X		X	X		
<i>Sarangesa seineri seineri</i> Strand, 1909				X	X	X	X			
<i>Spialia colotes transvaaliae</i> (Trimen), 1889								X		
<i>Spialia delagoae</i> (Trimen), 1898				X						
<i>Spialia diomus ferax</i> (Wallengren), 1863				X						
<i>Spialia dromus</i> (Plotz), 1884		X							X	
<i>Spialia mafa mafa</i> (Trimen), 1870				X	X	X				
<i>Spialia secessus</i> (Trimen), 1891		X								
<i>Spialia spio</i> (Linnaeus), 1764		X		X		X		X		X
<i>Tagiades flesus</i> (Fabricius), 1781		X	X	X	X	X	X	X	X	X
Totals: 612 taxa		472	60	144	119	111	89	131	126	96

CHAPTER 10 : APPENDIX 1
LIST OF LEPIDOPTERA COLLECTED FROM BAROTSELAND

Lepidoptera specimens were collected from the Barotseland area by Rafael Chiwanda and Philip Mhlanga from 20 March to 4 April 1999. Localities collected were:

Ndau School transect: 15°25'41"S / 22°57'49"E
 Ndau School area: 15°25'S / 22°58'E
 Sefula: 15°23'11"S / 23°10'07"E
 Mongu: 15°17'46"S / 23°08'36"E
 Kalabo: 14°58'10"S / 22°38'27"E
 Kalabo, 5 km west: 14°54'58"S / 22°34'02"E

List of Species Collected (nomenclature follows Pennington 1994, second edition).

BUTTERFLIES

Family Nyphalidae

Sub-tribe Melantini

Melantis leda helena

Ypthima impura?

Tribe Acraeni

Acraea acerata

Acraea atergatis

Acraea atolmis

Acraea caldarena

Acraea encendon encendon

Acraea natalica

Tribe Charaxinae

Bybilia ilithya

Charaxes achamenes achamenes

Eurytela dryope angulata

Hamanumida daedalus

Neptis jordani

Neptis laeta

Precis antelope

Precis ceryne

Precis octavia sesamus

Precis oenone oenone

Family Lycaenidae

Tribe Hypolycaenini

Deudorix antalus

Eicochrysops trochilus

Freyeria trochylus

Hypolycaena phillipus

Lampides boeticus

Leptotes pulcher

Family Pieridae

Eurema brigitta brigitta

Eurema hapale

Mylothris agathina

Mylothris rubricosta rubricosta

Family Hesperidae

Gegenes niso niso

Pelopidas mathias

Platylesches shona

MOTHS

Macroglossium trochilus

Othreis materna

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CHAPTER 10 - APPENDIX 2 LEPIDOPTERA SPECIES COLLECTED FROM THE ZAMBEZI DELTA

Nicola Feltham

1. INTRODUCTION

As is the case with most wetlands world-wide, the biodiversity of the Zambezi Basin is under threat from increasing human population growth and associated impacts. Little is known about the biodiversity of this area, therefore it is important to document the species present in the basin so that, as human impact increases, changes in faunal population numbers and species occurrence may be monitored.

Butterflies have long been recognized as indicators of environmental health (Feltwell 1986, Kremen & Razafimahatratra 1990, New 1997). Ecological indicators, as defined by Noss (1990), are "species that signal effects of perturbations on a number of other species with similar habitat requirements". Although there are many other insect groups that may serve as ecological indicators (Brown 1991), a wide range of butterfly families are particularly good candidates for both practical and biological reasons – they are often involved in highly specific plant-herbivore and plant-pollinator interactions (Ehrlich & Raven 1964, Pullin 1995), and there is good taxonomic knowledge of butterflies and they are easy to identify in the field (Pollard & Yates 1993). The widespread butterfly population and species losses reported by many researchers (e.g. Pyle *et al.* 1981, New 1997), frequently as a consequence of habitat fragmentation, often reflect the decline of a number of other taxa with similar habitat requirements.

This study details butterfly species diversity in one of the four IUCN Zambezi Basin Wetlands Biodiversity Project areas, namely the wetlands of the lower Zambezi Delta in what is called the Marromeu Complex. The sites chosen are described, the butterfly species at each site catalogued and a brief description of the known distribution and environmental requirements of each butterfly species is given. Cognisance of the status of butterflies as environmental indicators is taken and brief conclusions about the condition of environmental health made on the basis of the findings.

2. SAMPLING SITES

2.1 Site A: Safrique

18°26'52" S / 35°53'46" E

Sampling took place in semi cultivated lands, a short walking distance from the village outskirts. Rice was the principal crop, but owing to the dry soil conditions, plants were very stunted. Sorghum was also growing in the fields. *Vigna* spp. were abundant in the grassland and banana plants and Ilala palms (*Hyphaene coriacea*) in the area provided sheltered habitats for insect species. Along the edges of the cultivated fields, *Typha* sp. grew very tall and formed a moist environment at ground level. The area falls into the "dry wet grasslands" of the Marromeu complex as small water channels cross the area, although not filled with any water at the time. The soil was dry, black loam. This area was sampled on two consecutive days.

The most common butterflies in the area were *Danaus chrysippus*, *Hyalites eponina*, *Papilio demodocus demodocus* and *Eurema brigitta brigitta*, all highly eurotopic species. *Bicyclus safitza* and *Ypthimiomorpha itonia* were only found in association with *Typha* sp.

2.2 Site B: Vila Nova

18°23'42" S / 35°54'27" E

This site, 10 km south of Marromeu town, was sampled on two consecutive days; traps were set with banana bait. The area was very swampy; a tributary bisected the area and tall papyrus and *Typha* grew at the water's edge. A small settlement was situated on one bank of the tributary and associated rice paddies had been planted very close to the water in one area of the site. Coconut, *Phoenix* palms and bananas grew on one bank. Very little habitat in the immediate vicinity of permanent bodies of water throughout the Marromeu complex remain completely uncultivated. As a result, it was logistically very difficult to locate sampling areas described as "swampy wet grasslands" that were completely free of human interference. *Neptis laeta*

was particularly common here as was *Amauris ochlea*. The traps failed to catch anything except four *Bicyclus safitza safitza* individuals. *Bebearia orientis orientis* was found in association with its larval host, *Phoenix reclinata* (wild date palm), and also flying around banana trees.

2.3 Site C: River bank along the Zambezi

3 km range from Marromeu factory

Much of the day was spent observing insects from a canoe over an area which extended up and down from the factory in Marromeu. Very few butterflies were seen over the water or at the water's edge (from 9.00 to 11.00 only three butterfly individuals were observed, these being the common African Monarch and *H. eponina*). *Papilio demodocus demodocus* and *P. dardanus cenea* individuals were common around a small village on the river bank south of Marromeu. *Eurytela dryope* was seen flying around its larval host, *Ricinus communis* (the castor oil plant). The vegetation was typical of this environment: *Salvinia* sp., *Eichornia* sp., *Ipomea* sp. (?) and other water weeds predominated at the water's edge. Farther from the water, grass grew in rank stands. Where there was human habitation, common weeds such as *Bidens pilosa*, *Ageratum houstonianum*, *Tagetes minuta* and *Senecio* sp. grew in abundance around the houses and in the areas cultivated with vegetables, sugarcane and *Ricinus communis*.

2.4 Site D: River bank, 4 and 6 km south of Marromeu

18°18'18" S / 35°59'58" E

18°19'51" S / 36°01'25" E

As over the area covered at Site C, very few butterflies were seen in the vicinity of the river, except around human habitation where crops had been planted and plant weeds flourished. *Danaus chrysippus aegyptius* and *Hyalites eponina* were the only species seen with any regularity.

2.5 Site E: Bambani Area

18°18'09" S / 35°53'21" E

Like Site A, this area can be described as "dry wet grassland". Short grassland and small water channels made up this area, again depleted in butterfly fauna. Although nearby areas had been cultivated, the site itself was not. Relatively high abundance of blues and skippers is perhaps a reflection of the cropped vegetation and the presence of larval food plants, *Indigofera* sp (Clover Blue), *Oxalis corniculata* (Sooty Blue) and water-side grasses (the skippers).

2.6 Site F: Palm grove, north of Marromeu

18°13'05" S / 35°46'21" E

Undisturbed palm savanna, free of human habitation was a particularly difficult habitat to find in the Marromeu complex. Site F can perhaps be described as a palm grove since the ground beneath the coconut and Ilala palms was heavily cultivated with sugar-cane and sorghum. Around the houses, weed plants (in particular *Ageratum houstonianum*) grew in abundance. Traps set here with banana bait and left overnight revealed no new species.

2.7 Site G - Palm savanna, south of Marromeu

18°28'08" S / 35°53'43" E

This site is situated 3-4 km south of Safrique and was sampled over two consecutive days since it was relatively accessible, given the logistical problems of reaching palm savanna that was not inhabited. Both coconut and Ilala palms were abundant in the area; grass growth was dense. No water bodies were present and consequently the site was very dry. Sampling in this area was very poor with an average of three species being observed every hour; these butterflies being the eurytopic species present at each of the other sites. Traps yielded a *Melantia leda helena* and a *Papilio demodocus demodocus*. Significantly, it was observed that while walking through the homesteads to reach this area, far more butterflies were observed than when at the site. The pansies and other *M. leda helena* were caught around houses, vegetable gardens and other planted crops. *Asystasia gangetica* grew prolifically in vicinity of houses.

3. DISTRIBUTION AND ENVIRONMENTAL REQUIREMENTS

The various species found are described below. Table 1 shows the distribution between sites.

Appendix 10.2 Table 1 Butterfly species collected in the Marromeu area in June 1999
(* not common; ** common; *** very common).

Scientific name	Common name	Site							
		A	B	Ci	Cii	D	E	F	G
NYMPHALIDAE									
Danainae									
<i>Danaus (A.) chrysippus aegyptius</i>	African Monarch	***	**			**	**		***
<i>Amauris (A.) ochlea ochlea</i>	Novice Friar	***	***					***	**
Satyrinae									
<i>Bicyclus safitza safitza</i>	Common Bush Brown	**	***		***			**	
<i>Ypthimomorpha itonia</i>	Marsh Ringlet	**	**						**
<i>Melantis leda helena</i>	Common Evening Brown								*
Acraeinae									
<i>Hyalites (H.) eponina</i>	Dancing Acraea	***	***	***	***	**	***		
<i>Hyalites encedon encedon</i>	Common Mimic Acraea	*	**	*					
<i>Acraea (Stephenie) natalica natalica</i>	Natal Acraea		*						
Nymphalinae									
<i>Bebearia orientis orientis</i>	Eastern Palm Forester		**						
<i>Euphaedra neophron neophron</i>	Gold-banded Forester				**				
<i>Hamanumida daedalus</i> (sighted)	Guinea-fowl				**				
<i>Aterica galene theophane</i>	Forest-glade Nymph				*				
<i>Neptis jordani</i>	Jordan's Sailor						**		
<i>Neptis laeta</i>	Common Sailor		***					**	
<i>Byblia anvatarata acheloia</i>	Common Joker							*	
<i>Eurytela dryope angulata</i>	Golden Piper			*				*	
<i>Hypolimnas misippus</i>	Common Diadem			*					
<i>Precis (Junonia) oenone oenone</i>	Blue Pansy			*					
<i>Precis (J.) natalica natalica</i>	Brown Pansy								*
<i>Precis (J.) orithya madagascariensis</i>	Eyed Pansy	*						**	*
<i>Vanessa (Cynthia) cardui</i>	Painted Lady		*					*	
LYCAENIDAE									
Miletinae									
<i>Lachnocnema bibulus</i>	Common Woolly Legs							**	
<i>Lachnocnema durbani</i>	D'Urban's Woolly Legs	*							
Polyommatainae									
<i>Leptotes pirithous / brevidentatus</i>	Common Blue	*							
<i>Azanus natalensis</i>	Natal Spotted Blue					*			

Scientific name	Common name	Site								
		A	B	Ci	Cii	D	E	F	G	
<i>Euchrysops</i> sp.									*	
<i>Euchrysops malathana</i>	Common Smoky Blue			*	*					
<i>Euchrysops osiris</i>	Osiris Smoky Blue	**								
<i>Euchrysops barkeri</i>	Barker's Smoky Blue	*								
<i>Eicochrysops hippocrates</i>	White-tipped Blue			*						
<i>Zizeeria knysna</i>	Sooty Blue						**			
<i>Zizina antanossa</i> (?)	Clover Blue	*					**		**	
<i>Freyia trochylus</i>	Grass Jewel Blue		*							
PIERIDAE										
Pierinae										
<i>Catopsilia florella</i>	African Migrant	*								
<i>Eurema (M.) brigitta brigitta</i>	Broad-bordered Grass Yellow	***	***		***	**		***	***	
<i>Belenois creona severina</i>	African Common White							**		
<i>Mylothris agathina</i>	Common Dotted Border	***		**				***	***	
<i>Leptosia alcesta inalcesta</i>	African Wood White							*		
<i>Appias epaphia contracta</i>	Diverse White	**	**							
PAPIOLIONIDAE										
Papiolioninae										
<i>Papilio demodocus demodocus</i>	Citrus Swallowtail	***							***	
<i>Papilio dardanus cenea</i>	Mocker Swallowtail			**						
<i>Papilio nireus</i> (sighted)	Green-banded Swallowtail									
HESPERIIDAE										
Pyrginae										
<i>Spialia spio</i> (?)	Mountain Sandman		*							
Hesperiinae										
<i>Borbo fallax</i> (?)	False Swift						*			
<i>Borbo fatuellus fatuellus</i>	Long-horned Swift		*							
<i>Pelopidas thrax inconspicua</i>	White Banded Swift		*							
<i>Parnara monasi</i> (?)	Water Watchman						*			

Danaus (A.) chrysippus aegyptius

African Monarch

A very common butterfly that occurs all through the Afrotropical region and beyond. The species flies throughout the year at almost all altitudes and in most habitats. Larval host: members of Asclepiadaceae family.

Amauris (A.) ochlea ochlea

Novice Friar

A widespread species in the eastern portion of Africa, particularly in coastal forests of KwaZulu-Natal and Mozambique. Although widespread, this species is not as common as others in the genus and in some years emerges in very small numbers. It is generally more common during the summer months so it is perhaps

surprising that the butterfly was so abundant during the sampling period (winter) around Marromeu. Larval host: members of Asclepiadaceae family.

Bicyclus safitza safitza

Common Bush Brown

This species is very common throughout the Afrotropical region, particularly in rainforests. Individuals were caught in traps set with banana bait at Site B, Vila Nova. Larval host: grasses, in particular *Ehrharta erecta*.

Ypthimomorpha itonia

Marsh Ringlet

This butterfly is found along the eastern border of Zimbabwe and in Mozambique, usually in marshy places. Larval host: not confirmed, but possibly waterside grasses.

Melantis leda helena

Common Evening Brown

The species has an extensive range over the Afrotropical, Palaearctic and Indo-Australian regions. This particular subspecies occurs in a wide diversity of habitats; its range extends from wooded areas in Mozambique to coastal bush in the Transkei to the bushveld of northern South Africa, Zimbabwe, Botswana and N Namibia. This subspecies flies year-round, but is more plentiful during winter. Larval host: bristle grasses, kikuyu grass, sugar cane, *Cynodon* spp.

Hyalites (H.) eponina,

Dancing Acraea

This species is described in Pennington's Butterflies (Pringle *et al.* 1994) as being extremely common, widespread throughout the Afrotropical region and ubiquitous along the eastern wide of southern Africa. Indeed, this was the most abundant butterfly on the wing in the Marromeu complex during the study period. Larval host: *Hermannia* and *Triumfetta* spp.

Hyalites encedon encedon

Common Mimic Acraea

This butterfly is found throughout most of the eastern parts of southern Africa at all times of the year and is particularly common along the coastal areas of Natal and Mozambique. Larval host: *Commelina* spp.

Acraea (Stephenie) natalica natalica

Natal Acraea

This is another very common species that is found along the eastern side of southern Africa, most often in wooded terrain. Larval host: members of Passifloraceae family.

Bebearia orientis orientis

Eastern Palm Forester

This subspecies is widespread in Mozambique and has also been recorded along the eastern Zimbabwe border. Individuals were observed in the Marromeu complex in association with palm trees, the larval host-plant and caught in traps set at Site F. Larval host: *Phoenix reclinata* (wild date palm).

Euphaedra neophron neophron

Gold-banded Forester

This species is widespread in Mozambique and also occurs along the eastern border of Zimbabwe. Although Pare has described the food plant as occurring abundantly along the middle part of the Zambezi River and its tributaries (Pringle *et al.* 1994), this species was not found along the Zambezi in the Marromeu complex, but only in the forests away from the water's edge. Larval host: members of the Sapindaceae family

Hamanumida daedalus

Guinea-fowl

This butterfly is very common in Zimbabwe and Mozambique and also occurs in the Natal Midlands, Swaziland, northern parts of South Africa, N Namibia and Botswana. It flies throughout the year. Larval host: members of the Combretaceae family.

Aterica galene theophane

Forest-glade Nymph

This species is widespread in Mozambique, common in the Dondo and Savane forests (Pringle *et al.* 1994) and also occurs along parts of the E Zimbabwe border. Larval host: members of the Combretaceae family.

- Neptis jordani* Jordan's Sailor
Specimens of this species have been recorded before from Dondo, Buzi River and Moribane forest in Mozambique and at specific spots in Zimbabwe. Larval host: not confirmed.
- Neptis laeta* Common Sailor
This is the most widespread and common southern African *Neptis*. It was particularly common at Site B. Larval host: various plants, including *Dalbergia*, *Brachystegia boehmii*, *Albizia adianthifolia* and *Acalypha* spp.
- Byblia anvatarata acheloia* Common Joker
This butterfly is common across the eastern coast of southern Africa to Zimbabwe and N Namibia. Although usually observed throughout the year, few individuals of this species were observed. Larval host: members of Euphorbiaceae family.
- Eurytela dryope angulata* Golden Piper
This species is not nearly as common as *E. hiarbas*. It is to be found along the KwaZulu Natal coast, northern parts of South Africa, throughout Zimbabwe and Mozambique. Larval host: *Ricinus communis* (castor oil plant).
- Hypolimnias misippus* Common Diadem
An interesting mimic of other species, this butterfly is widespread throughout the Afrotropical region. Larval host: *Ageratum houstonianum* (floss flower), *Asystasia gangetica*.
- Precis (Junonia) oenone oenone* Blue Pansy
Another widespread species, this butterfly is common in most of southern Africa and flies throughout the year. Larval host: members of Acanthaceae family including *Asystasia gangetica*.
- Precis (J.) natalica natalica* Brown Pansy
This species occurs widely over Zimbabwe and Mozambique and is commonly seen in Natal throughout the year. Larval host: members of Acanthaceae family including *Asystasia gangetica*.
- Precis (J.) orithya madagascariensis* Eyed Pansy
Although these butterflies are generally not as common as others in the genus, individuals of this species were seen more regularly around Marromeu than *P. oenone* and *P. natalica*. Larval host: members of Acanthaceae family and *Plectranthus* spp.
- Vanessa (Cynthia) cardui* Painted Lady
This highly ubiquitous species is known throughout the world. Larval host: numerous plants, many of which are regarded as weeds (e.g. thistles).
- Lachnocnema bibulus* Common Woolly Legs
Found in woody and open savanna habitats throughout the eastern portions of the subcontinent, this species is regarded as being locally common and on the wing all year-round. Larval host: Psyllids (Homoptera).
- Lachnocnema durbani* D'Urban's Woolly Legs
Similar distribution and status to common woolly leg butterfly. Larval host: Coccids and membracids (Homoptera).
- Leptotes pirithous / brevidentatus* Common Blue/Short-toothed Blue
Species of this genus are difficult to distinguish from one another. *L. pirithous* is common almost everywhere in southern Africa and its distribution extends into Europe and even Asia. *L. brevidentatus* is similarly well distributed and coexists with *L. pirithous* down the east side of South Africa. This species does not appear
-

to have been previously collected from Mozambique. Larval host: *Plumbago auriculata* and various members of Fabaceae family.

Azanus natalensis

Natal Spotted Blue

Although this species is commonly found in thornveld in KwaZulu-Natal, the northern regions of South Africa and the eastern parts of Zimbabwe, it appears that it has not been collected before in Mozambique (it is likely though that the specimen is an alternative species of *Azanus*). Larval host: *Acacia* spp.

Euchrysops sp.

Species remains unidentified and therefore its distribution is unknown.

Euchrysops malathana

Common Smoky Blue

This inconspicuous blue butterfly is described in Pringle *et al.* 1994 as abundant in many parts of southern Africa, but Mozambique is not included in its distribution. Larval host: various *Vigna* spp. (Fabaceae family).

Euchrysops osiris

Osiris Smoky Blue

This species is seldom seen in large numbers and is more commonly found in Zimbabwe than Mozambique. Larval host: various *Vigna* spp. (Fabaceae family).

Euchrysops barkeri

Barker's Smokey Blue

Although common in localised parts of South Africa, this species is rare in the northern parts of South Africa and has only been collected in Zimbabwe and Mozambique on a limited number of occasions. Larval host: various *Vigna* spp. (Fabaceae family).

Eicochrysops hippocrates

White-tipped Blue

This species is abundant in localized spots across a wide area of southern Africa. Larval host: *Polygonum* sp., *Rumex* sp.

Zizeeria knysn

Sooty Blue

Described as the most common of all small blues from southern Africa. Larval host: *Oxalis corniculata*, *Euphorbia* sp. and a variety of other plants.

Zizina antanossa (?)

Clover Blue

In comparison to *Z. knysa*, this species is rare, has a more restricted distribution and has not been described from Mozambique. Larval host: *Indigofera* spp., *Desmodium incanum*.

Freyia trochylus

Grass Jewel Blue

Although widespread in distribution, this inconspicuous species is not found often. Larval host: *Indigofera cryptantha*, *Heliotropium* sp.

Catopsilia florella

African Migrant

This species flies almost year-round and is often very abundant during seasonal migrations. It inhabits the whole of southern Africa. Larval host: various species of *Cassia* (Fabaceae).

Eurema (M.) brigitta brigitta

Broad-bordered Grass Yellow

This species is far more common than others in its the genus and indeed more common than most of the Pierids. Larval host: *Hypericum aethiopicum*, *Cassia mimosoides*.

Belenois creona severina

African Common White

Another very common butterfly, this species also is often seen in large scale migrations. Larval host: *Boscia* spp., *Capparis* spp., *Maerua angolensis*.

Mylothris agathina Common Dotted Border
The distribution of this common species has, in recent years been shown to be increasing as the species adapts to additional food plants. Larval host: *Tapinathus rubromarginatus*, *Erianthemum dregei*, *Tieghemia quinquenervia*, *Ximenia caffra*, *Osyris lanceolata*, *Colpoon compressum*.

Leptosia alcesta inalcesta African Wood White
This species is common from the KwaZulu-Natal coast through Swaziland, the northern parts of South Africa, Mozambique and into Zimbabwe. Larval host: *Capparis* spp.

Appias epaphia contracta Diverse White
This species is widespread throughout Africa. Larval host: *Boscia* spp, *Capparis* spp., *Maerua angolensis*.

Papilio demodocus demodocus Citrus Swallowtail
"Abundant everywhere and throughout the year in subtropical Africa is no exaggeration for this ubiquitous butterfly" (Pringle *et al.* 1994). Larval host: a wide variety of tree species including *Clausena anisata*, *Calodendrum capense*, *Vepris* spp. and citrus trees.

Papilio dardanus cenea form *cenea* Mocker Swallowtail
This is the most common form of this subspecies of butterfly and is widely distributed over the eastern parts of southern Africa. Larval host: a variety of tree species including *Clausena anisata*, *Xymalos monospora*, *Vepris* spp. and citrus trees.

Papilio nireus lyaeus Green-banded Swallowtail
This subspecies is widespread in KwaZulu-Natal, Swaziland, the northern regions of South Africa and Mozambique. Larval host: a wide variety of tree species including *Clausena anisata*, *Calodendrum capense*, *Vepris* spp. and citrus trees.

Spialia spio (?) Mountain Sandman
This is a very common skipper that inhabits most of southern Africa. Larval host: *Hermannia* spp., *Hibiscus* spp., *Triumfetta* spp.

Borbo fallax (?) False Swift
A commonly occurring skipper that is distributed over the eastern parts of southern Africa in particular. Larval host: *Ehrharta* sp.

Borbo fatuellus fatuellus Long-horned Swift
Another commonly occurring skipper especially in coastal bush. Larval host: *Ehrharta erecta* and *Setaria megaphylla*.

Pelopidas thrax inconspicua White Banded Swift
This species is widespread over the whole of Africa and known to occur very commonly along the Zambezi River. Larval host: *Imperata cylindrica* and *Ehrharta erecta*.

Parnara monasi (?) Water Watchman
This species has occasionally been recorded as far as Beira; it's distribution appears to be scattered across southern Africa. In suitable localities this species can be common in winter. Larval host: waterside grass.

4. DISCUSSION

To a certain extent, fluctuations in butterfly assemblage structure may be attributed to taxonomic variations and the associated seasonal, ecological and biological differences (New 1997). Indeed, weather and large-scale climatic patterns have long been recognized as major factors in population dynamics of small ectothermic animals (Andrewartha & Birch 1954). Butterflies, being heliotherms, are generally associated with fine, sunny weather (Shapiro 1975, Pollard 1988, Pollard & Yates 1993). too, gives good evidence for a causal relationship between butterfly abundance and weather.

It is unfortunate that the heavy rains that were experienced in Mozambique over late summer/early winter delayed our trip for over a month. It is almost certain that a greater number of butterfly species would have been recorded had sampling taken place earlier in the year when temperatures were warmer and winter not so far progressed. The species list for the Marromeu complex can not therefore be regarded as comprehensive as sampling needs to be carried out throughout the year to allow for seasonal fluctuations in species availability.

Season, weather and vegetation have been shown to be highly correlated (Warren 1985). It could therefore be argued that insect populations and their respective food supplies are responding to the same environmental variables and there is no real causal basis to the relationship between the two. Sparks and Parish (1995) and Feber *et al.* (1996) suggest this is unlikely and indeed, butterfly distribution did appear to be related to vegetation in the Marromeu complex (discussed below). However, changes in season remain paramount in determining butterfly presence in this and other areas (New 1997).

Butterfly utilization of plants, at least for nectar, appeared to be opportunistic. The plants with the most nectar-laden flowers tended to be exotic weeds and as a result more butterflies feed on them. Exotic plant presence indicated butterfly presence. The butterfly assemblage in the Marromeu complex seemed to be largely composed of highly vagile, migrant species whose distributions as generalists are influenced by abundant nectar sources. Jackson (1987) has noted preference for exotic nectar sources particularly by migratory species which may reasonably be expected to be more adaptable to a variety of food sources. These resources were located around human settlements; as is often the case, exotic weeds flourished in these areas of disturbance. This association with exotic weeds could however be a function of season (few indigenous plants flowering during winter) which reinforces the importance of sampling throughout the year. Low levels of species richness can also be attributed to the predominance of a limited number of crops, namely sugarcane and sorghum. Uncommon species and those with localized distributions were found by Jackson (1987) to prefer indigenous nectar plants. The distribution of more sedentary species (such as the Blues and Skippers) of the Marromeu complex appeared to be determined more by larval host plants presence.

Butterfly abundance and species diversity was also a consequence of microhabitat heterogeneity. Sparsely-vegetated patches of earth in warm, sunny and sheltered conditions have been described as being the most suitable for butterflies (for Nymphalids in particular; Vickery 1998). Such conditions prevailed in the villages where earth had been cleared around the houses and the natural vegetation thinned or removed for garden replacement.

To conclude, many of the butterfly species found in the Marromeu complex utilize exotic plant species which are pioneers of bare ground and areas of disturbance. These weeds flower prolifically and attract nectar-feeding insects, especially eurytopic butterflies. Owen (1971) reports that a remarkable proportion of common African butterflies now utilize agricultural weeds that have been introduced with crops as larval food-plants and these species have consequently expanded their range and increased their numbers. This suggests that an area such as the Marromeu complex where the natural vegetation has been disturbed to such a great extent, an assemblage of fewer, yet abundant, butterfly species is to be found. If butterflies are to be regarded as indicators of environmental health, there is concern for overall plant and animal species biodiversity in this part of the Zambezi Basin.

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CHAPTER 11

REVIEW OF AQUATIC INVERTEBRATES OF THE ZAMBEZI BASIN

Brian Marshall

11.1 INTRODUCTION

The invertebrates are an enormously diverse group of animals, falling into about 35 phyla (Barnes 1986) depending on the system of classification adopted. Some workers include the animal-like protists (Protozoa); others divide the Arthropoda into several different phyla, while the invertebrate chordates are also frequently included amongst them. Some of these phyla are very large; for example there are about 50,000 described molluscs and at least 750,000 arthropods. The greatest diversity of invertebrates occurs in the oceans and on land where the arthropods are the dominant forms. But they are also abundant in freshwater, where about 13 phyla are represented (Edmondson 1959, Durand & Lévêque 1980, 1981). Current thinking is that there may be 36-45 protozoan phyla (Corliss 1984, Margulis 1990) and 32-38 phyla of metazoan (animals) phyla (Minelli 1993) making a total of 68-83 phyla. Total number described varies, but Hammond's review (1992) seems to be well respected. Mollusca is considered to have over 100,000 species (Brusca & Brusca 1990), while the Insecta is estimated to have more than 950,000 species presently described (Hammond 1992). Large as these numbers are, they represent only the tip of the iceberg of invertebrate biodiversity, which is expected to be 10-30 million species (Hammond 1992).

Despite being far more diverse and abundant than vertebrates in aquatic systems, the ecology of invertebrates has generally been neglected in the Zambezi Basin. The reasons are obvious; the vertebrates are mostly relatively large and conspicuous (in the case of birds or mammals) or of importance as food or for recreation (especially fish). Furthermore, the vertebrates are much easier to identify and there is a wide range of guidebooks available to the layman. By contrast, invertebrates are much more difficult to identify and specialist knowledge is usually required. Invertebrate groups that have been studied in detail include the vectors of human or animal diseases like some gastropod molluscs or mosquitoes. Even in these species, though, investigations tend to be orientated to control measures and the prevention of disease transmission rather than towards biology or ecology.

This review must necessarily be an inadequate one. The literature on invertebrates is very extensive and sometimes rather specialised, and no one person can be familiar with all of it. In preparing this review, I have concentrated on invertebrates in ecosystems and on papers that describe the diversity and composition of invertebrate communities. Adequate coverage of the taxonomic literature would be impossible to achieve, and I have not attempted it.

One of the major difficulties in dealing with aquatic invertebrates in tropical Africa is the lack of adequate guidebooks. Fortunately, many groups are cosmopolitan and general books published elsewhere can be used to identify them at least to the level of family and, in some cases, to genus. One of the most useful books for African workers is the two-volume *Flore et Faune Aquatiques de l'Afrique Sahelo-Soudanienne* (Durand & Lévêque 1980, 1981). Its major drawback is that animals are identified only to family and generic level. Unfortunately, it is not readily available in anglophone Africa, including most of the Zambezi Basin, where in any case many would be deterred by the fact that it is written in French. Keys for the identification of southern African forms are

currently being prepared in South Africa and these should help to fill the need for English-language identification guides.

Another major difficulty is that many taxa are in need of revision. This becomes particularly important if an attempt to compare faunas in different systems is to be made. Workers in the field who lack taxonomic expertise often use names that have been used by someone else without any check on their accuracy. An example of this problem is the cyclopoid *Mesocyclops leuckarti*, which is referred to by this name in much of the literature from the Zambezi Basin. But a recent revision of the genus (Van der Velde 1984) showed that *M. leuckarti* does not occur in Africa. So which species is being referred to? No one knows, because reference collections are rarely made.

The most useful source book to the literature on African freshwater invertebrates is the bibliography produced by Davies, Davies, Frazer & Chutter (1982). This work has been used extensively in preparing this review and readers should refer to it for further references. Unfortunately, it carries references only to 1980 and there has been no subsequent revision.

Most invertebrate phyla include parasitic forms as well as free-living ones and in some cases (e.g. Platyhelminthes) the former are more important than the latter. Many human parasites that have an aquatic phase, or are transmitted by aquatic organisms, are responsible for diseases like bilharzia, malaria, river blindness, and so on. This review makes no attempt to deal with parasitic forms or the diseases that they might be responsible for, being restricted to free-living species only in order to keep it to a manageable size.

It would be highly desirable if checklists of the aquatic invertebrates of the Zambezi Basin could be produced. In practical terms this is very difficult because most groups have not been thoroughly collected, indeed the gaps in our knowledge of these animals are very striking. Furthermore, the taxonomic literature that would be needed for such an exercise is very scattered and much of it is in museum journals with a very limited distribution. Few libraries in the countries of the Zambezi Basin have the resources to obtain these papers. One of the major problems for workers in the basin is that most of the specimens are available in museums in Europe or North America and difficult to access and therefore effectively lost to local workers. However, good collections of certain groups are found in various institutions in South Africa.

11.2 INVERTEBRATE GROUPS

KINGDOM PROTISTA

The protists are single-celled organisms but with a complex structure, now generally grouped together as a separate kingdom but formerly treated as unicellular plants or animals. Although not generally regarded as invertebrates, they can be very important ecologically in pelagic ecosystems (Dumont 1986, Hecky & Kling 1981). The animal-like protists (protozoa) are heterotrophic, and free-living or parasitic. Free-living forms all live in an aqueous medium, which may include the interstitial water in the soil as well as water in ponds or lakes. The principal forms of free-living animal-like protists in freshwater include:

Phylum Rhizopoda: The rhizopods, also known as the Sarcodina, include the naked amoebas (e.g. *Chaos*) and testaceous forms, i.e. enclosed in a shell of some kind (e.g. *Diffugia*, *Chlamydomphrys*). The systematics of the group was said to be chaotic (Dragesco 1980) and is probably still in need of revision. Most of these amoebae are soil animals and there seems to have been little published

in Africa on forms living in a more typical aquatic environment. The bibliographies in Dragesco (1980) and Davies *et al.* (1982) suggest that most of the literature deals with free-living forms in the soil or with parasitic ones, and there seem to be few papers on truly aquatic forms. The paper by Green (1963) that discusses rhizopods in the Sokoto River in West Africa may contain some information relevant to the Zambezi system.

Phylum Actinopoda: This phylum includes the heliozoans (mostly freshwater) and radiolarians (mostly marine), both amoeboid animals frequently enclosed in a spherical siliceous skeleton. Their fine needle-like pseudopods (known as axopods) are greatly extended and radiate from the centre of the body. They may be floating as part of the zooplankton, or benthic, in which case they may be sessile, stalked forms. They are extremely delicate organisms and little is known about them, especially in Africa. Apart from some comments in Dragesco (1980) there seems to be nothing available about this group on the continent.

Phylum Ciliophora: The ciliates are a large, diverse and complex group with a great variety of sub-cellular microstructures. There are thought to be about 1000 species living in freshwater (Dragesco 1980) and they occur in almost any kind of aquatic habitat being free-living, sessile or parasitic. As with the other protozoan groups, there are few data on African ciliates and none on those of the Zambezi system. The papers by Dragesco (1966, 1970, 1972a, 1972b, 1973) may be of value.

KINGDOM ANIMALIA

Phylum Porifera: The sponges are an important group of animals in marine systems, but a few species occur widely in freshwater. In West Africa, there are thought to be about 11 species in 7 genera and two families (Boury-Esnault 1980) and the number in the Zambezi Basin is possibly similar. This group has not been studied in detail and the African literature is sparse. Papers that might have data of value to anyone working in the basin include some on sponges in the Bangweulu-Mweru system (Brien 1967, 1969, 1970a, 1970b), Lake Tanganyika (Brien 1974) and South Africa (Burton 1958). Papers from the Zambezi Basin itself include the description of a new genus and species from Lake Malawi (Brien 1972, 1973), raising the possibility that there may be a degree of endemism among the sponges of this lake. Penny (1986) notes that there are about 13 species in the Zambezi River, particularly near Victoria Falls. Other reports on sponges come from Lake Kariba (Begg & Junor 1971a, 1971b), the Mwenje dam, Zimbabwe (De Drago 1976) and Namibia. Two unidentified species have been recorded from the Kwando and Chobe rivers, and another from the Kavango River (Curtis 1991).

Phylum Cnidaria: The members of this phylum (also known as the Coelenterata) are almost exclusively marine, being represented in freshwater only by the hydras and some medusae. The hydras live in small streams and pools and are little known; virtually nothing has been published about the African forms, apart from some taxonomic descriptions from Kenya (Cox & Young 1973), the Congo (Semal-van Gansen 1953) and South Africa (Omer-Cooper 1964). It is possible that the species described in these papers might occur in the Zambezi Basin, but more work remains to be done.

Much more has been done on the medusae, of which there is only one African genus, *Limnocooida*, with only two species, *L. tanganyicae* and *L. indica* (Goy 1980). The former is the only one reported from the Zambezi Basin (Jordaan 1935, Pitman 1965, Begg & Junor 1971b, Oldewage & Shafir 1991, Curtis 1991). Mills (1973), who reported on a population explosion in the Mwenda estuary, Lake Kariba, is the only author to have presented any quantitative data on this species. Edney (1939) published a brief account of the behaviour of *Limnocooida* and its responses to external stimuli.

Phylum Platyhelminthes: This phylum is best known for its parasitic forms, which include the flukes (Monogenea and Trematoda) and the tapeworms (Cestoda). Many of these parasites are transmitted by aquatic vectors and are responsible for a number of diseases in animals and humans. A considerable effort has been made to control bilharzia and liver flukes, among others, and there is a considerable literature on these parasitic flukes (see Chapter 8). There is one free-living platyhelminth class, the Turbellaria, which are abundant animals in suitable habitat, but they are inconspicuous and little is known about the African species (Gourbault 1980). Curtis (1991) reported that an unidentified species had been collected from rainwater pools in the eastern Caprivi, but there seem to be no other reports about turbellarians in the Zambezi Basin. Some papers that might be useful include Ball (1974), de Beauchamp (1951), Kawakatsu (1972), Marcus (1955, 1970), Young (1976) and Young & Young (1974). Weir (1969) described the fauna of some temporary pools in the Hwange National Park, Zimbabwe, from which he recorded two turbellarians, *Castrada* sp. and *Phaenocerca foliacea*, each of which occurred in five out of 12 pools.

Phylum Nemertea: Freshwater nemerteans are widely distributed but inconspicuous animals that live upon the vegetation in rivers, streams and lakes, or amongst detritus on the bottom. They are thought to be related to the flatworms (Turbellaria) and there is only a single freshwater genus, *Prostoma*. Some work has been done on nemerteans in Kenya (Gibson & Young 1974, Young & Gibson 1975), but there are no reports from anywhere else in Africa.

Phylum Gastrotricha: A small phylum of about 460 species, including both marine and freshwater forms. They are said to be common animals in ponds, streams and lakes and most are benthic (Brunson 1959). There are no data from Africa.

Phylum Nemata (Nematoda): The nematodes (roundworms) are amongst the most widely distributed and abundant of all animals. Free-living nematodes occur in almost any habitat and there are many parasitic forms that attack almost every kind of plant and animal. Aquatic vectors transmit many of the parasitic forms that cause diseases in humans and animals. The most important of these is river blindness (onchocerciasis), which is widespread in west and central Africa, and much of the literature on freshwater nematodes in Africa stems from efforts to control this disease.

There is some literature on parasitic nematodes in freshwater fish (Khalil 1971, Khalil & Polling 1997). The references Andrassy (1984) and Jairajpuri & Ahmad (1992) should also be mentioned.

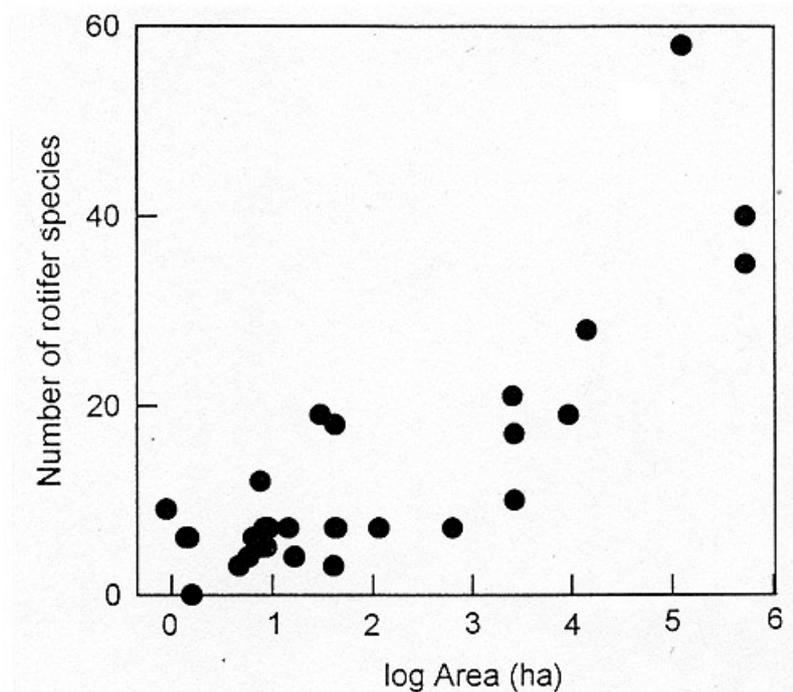
Despite the fact that they are abundant and widespread, very little is known about free-living aquatic nematodes in Africa, possibly because they are very difficult to identify. The literature is very sparse and nothing that could be related to the Zambezi Basin was found, apart from a paper by Coomans, Rashid & Heyns (1995) that presumably refers to free-living nematodes in the Okavango Delta, Botswana. In a comment that could apply to whole basin, Curtis (1991) noted that little was known about free-living nematodes in Namibian waters and that there might be a number of endemic species in the country. Some works that might contain relevant data include Andrassy (1970), Heyns (1976) and Meyl (1957).

Phylum Rotifera: The rotifers (also known as Rotatoria), or wheel-animalcules, are microscopic animals, usually about 100-600 μm in size, occasionally reaching 1 mm (Pourriot 1980). The vast majority live in freshwater where they may be sessile or free-living, and only a few species are marine or parasitic. They are important constituents of the zooplankton in lakes. In the Zambezi Basin they have mostly been investigated as components of the plankton. With the exception of

Green & Carey (1965), who examined samples from the Kafue River, all of the work on rotifers comes from lakes and reservoirs, especially Lake Kariba. A list of rotifers in Lake Liambezi is given in Seaman *et al.* (1978), who also briefly describe their vertical migration over a 24-hour period. Dudley (pers. comm.) notes that there are 12 species known from Malawi, although the majority of these are in Lake Chilwa, just outside the basin.

Some of the earliest records of rotifers from Lake Kariba appear in Thomasson (1965), while Bowmaker (1973) gives some quantitative data on rotifers in the zooplankton. These data are of particular interest since they pre-date the introduction of kapenta, *Limnothrissa miodon*, into the lake. At that time rotifers were relatively insignificant in the plankton, making up 3% by weight. This situation changed after the sardines eliminated the larger crustacean zooplankton and rotifers now make up over 80% of the zooplankton (Marshall 1991, 1997). Andersson & Stenson (1989) briefly noted the possible impact of predation on the morphology of *Brachionus calcarus* in the lake. Other studies were concerned with their distribution in the lake (Magadza 1980; Green 1985) and the seasonal cycle of *Keratella cochlearis* in relation to thermal stratification (Begg 1974), or their diurnal movements in relation to predation by kapenta (Begg 1976). Finally, some data on rotifers is available from a series of small impoundments near Marondera and in the Nyanga District, Zimbabwe (Green 1990) and from Lake Chivero (formerly Lake McIlwaine) and Cleveland dam, both near Harare (Elenbaas & Grundel 1994). It is possible to prepare lists of rotifers from these papers (Table 11.1) but few clear patterns are evident, apart from the much greater number in Lake Kariba. This is to be expected since there seems to be an association between the size of a water body and the number of rotifer species (Figure 11.1). The most widespread species found in all of these waters, was *K. cochlearis*, which made up 74-94% of the rotifers in Lake Kariba and 20-84% of those in the other reservoirs. This species has been discussed in relation to its entire African distribution (Green 1987) and some data from Zimbabwe are included in that paper.

Figure 11.1 The number of rotifer species in various lakes and reservoirs in relation to their surface area. Data from various sources in Green (1990) and Elenbaas & Grundel (1994).



Phylum Annelida: The annelids (segmented worms) are most abundant in the oceans but two groups, the Oligochaeta and the Hirudinea, are predominantly freshwater forms. There are five families of aquatic oligochaetes and they are important members of the benthos in rivers and lakes (Brinkhurst 1966, Brinkhurst & Jamieson 1973, Lauzanne 1980). Despite being abundant animals, they have not been investigated in much detail anywhere in the Zambezi Basin, apart from some work done in Lake Chivero in Zimbabwe. Martin & Giani (1995) described a new species from Lake Malawi. Other references for the region are Beddard (1908) and Martin & Giani (1995).

Lake Chivero is highly eutrophic and the bottom sediments are rich in organic matter, conditions that favour oligochaetes, which are able to tolerate the anoxic conditions that occur at the mud-water interface. The principal species in the lake were *Branchiura sowerbyi* and *Limnodrilus hoffmeisteri* with occasional specimens of *Dero digitata* (Brinkhurst 1970). They preferred to live in sediments with organic detritus and were abundant at depths ranging from 2-20 m. They were able to invade the deeper sediments in winter when the lake was isothermal and were therefore the most abundant benthic species in this zone (Marshall 1972, 1973, 1978, 1982). About thirty years later the benthos of the lake was re-investigated and oligochaetes were still abundant, although *Branchiura sowerbyi* seemed to be absent, probably reflecting the increasing severity of pollution in the lake (Marshall 1995).

The only other data on oligochaetes in the Zambezi Basin come from lakes Kariba and Liambezi. Bowmaker (1973) found that there was a greater diversity in Lake Kariba than in Lake Chivero, with *Aulodrilus pigueti*, *Branchiodrilus hortensis*, *Branchiura sowerbyi* and *Dero dorsalis* being present. They made up about 20-30% by weight of the benthos and were presumably eaten by fish, although there was no evidence of them in any stomach contents. The lack of resistant species like *Limnodrilus hoffmeisteri*, which is capable of surviving in extremely polluted situations, reflects the unpolluted state of Lake Kariba. *Ilyodrilus* and *Limnodrilus* were present at most stations in Lake Liambezi, sometimes in quite large numbers (>1000 per m²). This was particularly the case in areas where the bottom was strewn with hippopotamus dung (Seaman *et al.* 1978), again reflecting the ability of oligochaetes to live in areas with high organic matter and low oxygen.

Another important group of aquatic annelids are the Hirudinea (leeches) which are widespread and sometimes abundant animals. They seem to have been almost completely overlooked in the basin, except perhaps for some data from Namibia where two families and 15 species are known. *Placobdelloides jaegerskioldi* and *Asiaticobdella fenestrata* were found only in the eastern Caprivi (Oosthuizen & Curtis 1990, Curtis 1991) but might be expected elsewhere in the Okavango or Upper Zambezi systems. Publications that may have some useful data include Sawyer (1986), Sciachitano (1959, 1962, 1963) and Soós (1970).

Phylum Ectoprocta: The moss animals are generally placed in the phylum Bryozoa but it is often suggested that the phylum should be split into the Endoprocta (entirely marine) and Ectoprocta (entirely freshwater). They are inconspicuous, sessile branched animals that superficially resemble algae or moss (Wiebach 1980). They are largely overlooked and may be more common than generally supposed. Very little is known about these animals in the Zambezi Basin, apart from some records for Namibia where five species in two families have been recorded. The three species of *Plumatella* (*P. emarginata*, *P. punctata* and *P. repens*) are cosmopolitan, while *Lophopodella capensis* and *L. thomasi* occur elsewhere in southern Africa (Curtis 1991).

Table 11.1.1. The genera of rotifers from some water bodies (mostly dams) in the Zambezi Basin. The numbers indicate the numbers of species of each genus in each water body. Data from Green (1985, 1990), Seaman *et al.* (1978) and Elenbaas & Grundel (1994).

Altitude (m)	485	929	1260	1340	1350	1350	Edinburgh	Jobertii	Gwasi	1420	1560	1600	Nyambuya	Udu	Rhodes	1707	1768	1813	Claremont	1920	1951	2134	2255	2270	
	Lake Kariba	Lake Liambezi	Matoko (Sweet Valley)	Mtemwa	Lake Chivero	Edinburgh	Jobertii	Gwasi	Cleveland	Nyambuya	Udu	Rhodes	Moodie	Claremont	Pardon	Gulliver	Mare	Troutbeck	Large Connamara	Small Connamara					
<i>Aneuraeopsis</i>	2	1	1	1	1	1	1	1																	
<i>Ascomerpha</i>	1											1													
<i>Asplanachia</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Brachionus</i>	4	4	2	2	3	2	2	5																	
<i>Cephalodella</i>																									
<i>Cobarella</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Conochilus</i>																									
<i>Epiphanes</i>	1				1																				
<i>Enchlamis</i>	1				1				1																
<i>Filinia</i>	3	1	1	1	1	1	1	2	2																
<i>Gastropus</i>																									
<i>Hexarthra</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Keratella</i>	2	2	1	1	2	1	2	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>Lecane</i>	6	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	3	
<i>Lepidella</i>																									
<i>Mytilina</i>																									
<i>Polyarthra</i>	1				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Pompholyx</i>																									
<i>Synchaeta</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tetramastix</i>																									
<i>Trichocerca</i>	5	1	1	2	3	2	3	2	2	1	3	1	2	3	2	2	2	1	1	2	2	1	1	1	1
<i>Trichotria</i>	1																								
Totals	30	15	6	7	17	9	5	6	19	4	7	6	7	7	7	5	5	4	3	11					

Phylum Mollusca: The molluscs are an important group of freshwater invertebrates and the gastropods have been studied in some detail because of their importance as vectors of parasites that cause human and animal diseases. They have been reviewed separately (Chapter 8).

Phylum Tardigrada: The systematic position of the tardigrades (water bears) is unclear, some authors treat them as allies of the annelids, others the arthropods, but they are probably best retained as a separate phylum (Barnes 1986). They are minute animals usually about 0.3-0.5 mm long, although some reach 1.2 mm. They mostly inhabit the water film surrounding the leaves of mosses and lichens but some are freshwater species, living in bottom detritus or on algae and aquatic mosses. Because of their small size, they are rarely encountered and nothing is known about them in the Zambezi Basin. One of the few papers on African tardigrads is Iharos (1969) but the review by Ramazzotti (1972) may mention African species.

Phylum Arthropoda: The arthropods are an enormous assemblage of animals with at least 750,000 described species, three times the number of all other animals combined (Barnes 1986). The adaptive diversity of the arthropods has enabled them to live in almost all habitats and they are the most successful of the invaders of the terrestrial environment. Nevertheless, they have also been very successful in aquatic environments and are diverse and numerous animals in all freshwater systems.

Subphylum Chelicerata: The chelicerates are primarily terrestrial being represented by well-known forms like the spiders, the scorpions and their allies, and the ticks and mites. Some mites have become aquatic and they can be quite abundant at times. In spite of this, little is known about them in Africa and no data are available from the Zambezi Basin. A useful paper is that of Jansen van Rensburg (1976) which gives a key to the families of water mites in the Afrotropical region. Other papers that describe water mites from central and South Africa and should be of some value to workers in the Zambezi Basin include Bader (1968), Dippenaar-Schoeman & Jocqué (1997), Viets (1959, 1968, 1971, 1980), Viets & Böttger (1974a, 1974b) as well a general review of African water-mites (Viets 1953).

Many spiders are associated with water, but there are no truly aquatic species in Africa (Lawrence 1970). None are able to swim but they can dive below the surface for short periods or run rapidly on the surface. The best-known semi-aquatic spiders are the fish-eaters, *Thalassius* spp., which are large animals able to catch small fish and tadpoles. There are several species in this genus and they are widely distributed but little known.

Subphylum Crustacea: The crustaceans are the only arthropod subphylum that is primarily aquatic. The majority of its 42,000+ species is marine but there are numerous freshwater forms. Functionally, but not taxonomically, the subphylum can be split into three groups: the fairy shrimps and their allies that live in seasonal pools, the microcrustacea, and the relatively large decapods. There are also a number of parasitic species, especially among the Copepoda, which infest fish and crabs, but these have not been taken into account here. A general introduction to the African crustaceans can be found in Rey & Saint-Jean (1980), Dussart (1980, 1989), Kiss (1980) and Monod (1980). Dussart (1989) gives a more detailed list of the calanoid copepods. The known crustacean fauna of Malawi is about 130 species, including Decapoda (C. Dudley, pers. comm.).

(a) *Crustacea of seasonal pools*

The crustacea that live in seasonal pools are primarily the classes Branchiopoda (order Anostraca) (fairy shrimps) and Ostracoda (seed shrimps). They are mostly ephemeral and survive periods of

drought by the production of resistant eggs. Consequently, they tend to be most numerous in arid or semi-arid areas. Of the countries in the Zambezi Basin, Namibia seems to have the greatest diversity with some 35 ostracod species, of which 18 may be endemic (Curtis 1991). At least five of them are confined to very arid regions of Namibia and Botswana while only ten are widespread in Africa.

Little is known about these animals elsewhere in the basin. General reviews of these groups include Kiss (1980) and Rey & Saint-Jean (1980), while other works include the description of a new species from Zimbabwe (Hartland-Rowe 1969) and a detailed review of the family Streptocephalidae in Africa (Hamer, Brendonck, Coomans & Appleton 1994a, 1994b). These papers suggest that about eight species of *Streptocephalus* may occur in the basin: *S. caffer* (Zimbabwe), *S. macrourus* (Botswana, Namibia), *S. indistinctus* (Zimbabwe, Namibia), *S. ovamboensis* (Namibia), *S. trifidus* (Zimbabwe), *S. vitreus* (Zimbabwe) and *S. cladophorus* (Namibia). Another species, *S. wirminghausi* has also been collected from pans in the middle Zambezi valley in Zimbabwe (Hamer 1994). Other genera commonly found in seasonal pools, including *Branchipodopsis* and *Triops* have also been reviewed recently (Truxal 1990, Hamer & Appleton 1996, Hamer & Rayner 1995). The authors point out that very little collecting has been done outside South Africa and Namibia, and there may be other species elsewhere in the basin.

Weir (1969) recorded *S. vitreus* and *Caenasteriella australis* in pools in the Hwange National Park, Zimbabwe, where they occurred in six of the 12 pools that were sampled. There seems to be no other data on these species from the Zambezi Basin.

(b) *Microcrustacea*

The microcrustacea are principally found amongst the classes Copepoda (principally the orders Calanoida and Cyclopoida), Branchipoda (suborder Cladocera) and Ostracoda. Rey & Saint-Jean (1980) give a general introduction to the African cladocerans, while Dussart (1980) and Kiss (1980) do the same for the copepods and ostracods, respectively. More specialised papers include Rayner (1992, 1994) and Martens (1984, 1990).

They are generally sparse in running waters, although some records are available from the Zambezi and Kafue rivers (Jackson 1961, Hall, Davies & Valente 1976, Green & Carey 1965). Similar species occurred at all sites, with *Diaphanosoma excisum*, *Daphnia* spp. and *Bosmina longirostris* being the most common cladocerans, and *Tropodiptomus* and *Mesocyclops* sp. the commonest copepods. Non-planktonic species included *Alona* sp. and *Chydorus* sp.

Most of the work on these microcrustaceans has been carried out in lakes and reservoirs. The zooplankton of Lake Kariba has been studied in considerable detail (see review by Marshall 1997) because of its importance as a food resource for the sardine *Limnothrissa miodon*, which now accounts for about 60-70% of the lake's fish production. Some data from the period before *Limnothrissa* were introduced are available in Bowmaker (1973) against which the changes brought about by the sardine can be assessed. These changes are typical of those that follow the introduction of planktivorous predators anywhere in the world and involve the elimination of larger species like daphniids and larger copepods until only small ones like *Bosmina* and rotifers are left (Table 11.2). The suggestion that these changes reflect a "stressed" ecosystem (the implied stress is high levels of DDT in the water) made by Berg (1995) can therefore be discounted.

Table 11.2. Changes in the relative abundance (%) of zooplankton in Lake Kariba, following the introduction of *Limnothrissa miodon* in 1967-68. Data from Marshall (1991).

	1967-68	1970	1972	1975-76
Diaptomids	14.3	0.2	0	+
Cyclopoids	4.7	12.5	10.1	13.8
Nauplius larvae	11.1	16.4	17.1	3.1
<i>Bosmina</i>	7.4	15.9	17.1	10.5
<i>Ceriodaphnia</i>	69.3	14.3	0	0.3
<i>Diaphanosoma</i>	2.2	0.2	0	+
Daphniids	0.9	0.2	0	0
Rotifers	+	40.3	55.7	72.3

+ = change, but unmeasured.

As in other lakes, the zooplankton make diurnal migrations up and down the water column and the sardines follow them closely (Begg 1976), which emphasises their importance as a food resource. Indeed, the condition and abundance of the kapenta closely follows the abundance of plankton (Cochrane 1984, Marshall 1988). From this efforts to determine the factors that influence the distribution and abundance of zooplankton were made, revealing the importance of the rivers and the nutrients they bring in to the lake (Magadza 1980, Marshall 1997, Masundire 1994). Other factors of importance were predation by the sardines (Masundire 1989a, 1991, 1992) and water transparency (Masundire 1989b).

The presence of kapenta in Lake Cabora Bassa has also focussed interest in its zooplankton. Its species composition is similar to that of Lake Kariba, with the larger species having been eliminated in open water and the small *Bosmina longirostris* being the dominant species (Gliwicz 1984, Mandima 1997). The impacts of predation were well illustrated by Gliwicz (1986a) who described a distinct lunar cycle amongst the zooplankton, which depended on the fact that the water of Lake Cabora Bassa is very turbid. At full moon, when light penetration was greatest, the kapenta were able to see the larger zooplankton and they were eliminated. As the moon waned, light penetration decreased and larger forms like *Diaphanosoma* at first, followed by *Daphnia*, began to appear. As the moon waxed this sequence was reversed. The crustacean zooplankton were also important in Lake Cabora Bassa because they filtered out clay particles and so influenced water transparency (Gliwicz 1986b).

Relatively little work has been done on the zooplankton of Lake Malawi, in spite of its large size. Jackson *et al.* (1963) gave a brief and mostly qualitative synopsis of the zooplankton community, and this was followed by Fryer (1957a, 1957b, 1957c). More information became available after the FAO fishery expansion project, which provided data on seasonal variation in abundance and vertical migration of the most abundant species (Degnbol & Mapila 1982). Twombly (1983) also investigated seasonal variation. Lake Malawi supports a number of pelagic fish species and the zooplankton is an important component of their diet (van Lissa 1982, Thompson & Irvine 1997). Most of the inshore fish species in the lake also utilise zooplankton at some stage of their lives, usually as juveniles (McKaye, Makwinja, Menyani & Mhone 1985).

A major advance in knowledge of the zooplankton of Lake Malawi was brought about by the ODA/SADC study of its pelagic resources. In this study the biomass, production, spatial distribution

and seasonal variation of the microcrustacea throughout the lake was investigated (Irvine 1995a, Irvine & Waya 1995). A comprehensive study of feeding in pelagic fish species demonstrated the importance of the zooplankton to fishery productivity (Allison, Thompson, Ngatunga & Bulirani 1995). Because of the success of *Limnothrissa* in lakes Kariba and Cabora Bassa it was suggested that this fish might be introduced into Lake Malawi, which would have altered the composition of its zooplankton (Turner 1982). This suggestion was severely criticised on the grounds that the impacts of a zooplanktivorous fish would cascade unpredictably throughout the fish community of the lake bringing about irreversible and possibly adverse changes (Eccles 1985, McKaye *et al.* 1985). Finally, the biology of the most important species, the copepod *Thermodiaptomus cunningtoni*, was studied in detail by Irvine, Waya & Hart 1995).

Elsewhere in the Zambezi Basin, zooplankton has been investigated in Lake Liambezi (Seaman *et al.* 1978), and in Lake Chivero and Cleveland Dam near Harare. The latter studies dramatically illustrate the effects of eutrophication, since the zooplankton density in eutrophic Lake Chivero was generally about three times more abundant than it was in the oligotrophic Cleveland Dam (Elenbaas & Grundel 1994). Magadza (1994) used zooplankton to assess the state of pollution in Lake Chivero. Zooplankton associations in a number of small reservoirs near Marondera and Nyanga, Zimbabwe, provide a comprehensive list of species from those area, while other data are available from three reservoirs elsewhere in Zimbabwe (Magadza 1977). Magadza (1981) also published a checklist of the free-living entomostraca (Copepoda and Cladocera) of Zambia. A discussion of the altitudinal distribution of crustacean zooplankton in Africa (Green 1995) includes data from his earlier work.

It is possible to prepare checklists of microcrustacea for some places in the Zambezi Basin (Table 11.3). In most cases, the number of species ranges from 10 to 19 and the presence of only 11 species in Lake Malawi is probably an artifact since it refers only to planktonic forms. The large number of species in the Kafue and Bangweulu systems comes about because of the inclusion of many non-planktonic forms, primarily in the family Chydoridae. This reflects the swampy nature of both these systems that allows these species to survive without being eliminated by fish.

(c) *Macrocrustacea: the Decapods*

The Decapoda, which include the crabs, crayfish and shrimps, are primarily marine but they do include a number of freshwater species. The identification of freshwater crabs is particularly difficult (Monod 1980) but there appears to be only one true freshwater genus, *Potamonautes*, in the Zambezi Basin. This is the common river crab and it is not clear how many species are present, although Curtis (1991) suggest that three species occur in Namibia. Little is known about their ecology, apart from an estimation of their abundance (Turnbull-Kemp 1960) and their importance as food for otters, trout and eels (Butler & Du Toit 1994, Butler & Marshall 1996) in streams in the Eastern Highlands of Zimbabwe. Records of crabs from the Zambezi Basin are given in Cumberlidge (1997).

The shrimp *Caradina nilotica* is widely distributed in Africa and occurs throughout the Zambezi Basin, but little is known about it. Some general observations on their presence in Lake Kariba were made by Begg & Junor (1971b). The pelagic shrimp *Limnocaradina tanganyicae* was said to have been introduced into Lake Kariba from Lake Tanganyika (Bell-Cross & Bell-Cross 1971) but its fate is unknown. Some exotic species, including the Louisiana Red Crawfish *Procambarus clarkii* (Zambia) and the giant Malaysian prawn *Macrobrachium rosenbergii* (Malawi and Zimbabwe) have been brought to the basin for aquaculture purposes (Mikkola 1996). *Macrobrachium* are known to have escaped from a fish farm at Kariba and they have been caught at various places in the lake but

they are unlikely to become established, as their larvae need to grow in saline water. *Procambarus* can breed in freshwater and has become a problem in Lake Naivasha, Kenya, by destroying beds of submerged macrophytes that were important breeding areas for fish and reducing the numbers of leeches, clams and other invertebrates (Harper, Mavuti & Muchiri 1994). So far, there is no evidence that alien decapods have escaped into any natural systems in the basin, but the situation needs to be monitored closely.

Table 11.3. The microcrustacea of some waters in the Zambezi Basin. Data from Twombly (1983), Irvine (1995a), Green (1985, 1990), Elenbaas & Grundel (1994), Seaman *et al.* (1978), Magadza (1981) and Curtis (1991).

Group / species	Lake Malawi	Lake Kariba	Lake Chivero	Cleveland Dam	Marondera	Nyanga	Lake Liambezi	Zambia (Kafue system)	Lake Bangweulu	Namibia (East Caprivi & Kavango R.
Calanoida: Diaptomidae										
<i>Tropodiaptomus cunningtoni</i>	●									
<i>Tropodiaptomus hutchinsoni</i>		●						●		
<i>Tropodiaptomus kraepelini</i>	●	●						●		
<i>Tropodiaptomus longispinis</i>									●	
<i>Tropodiaptomus simplex</i>									●	
<i>Tropodiaptomus worthingtoni</i>			●	●	●	●				
<i>Tropodiaptomus sp.nov.</i>										●
<i>Thermodiaptomus congruens</i>							●			●
<i>Thermodiaptomus mixtus</i>			●	●	●					
<i>Thermodiaptomus syngenes</i>		●						●		
<i>Lovenula falcifera</i>										●
Cyclopoida: Cyclopidae										
<i>Afrocylops gibsoni</i>					●					
<i>Cryptocyclops inopinatus</i>										●
<i>Cryptocyclops linjanticus</i>								●	●	
<i>Tropocyclops confinis</i>								●		
<i>Tropocyclops prasinus</i>								●	●	
<i>Tropocyclops tenellus</i>					●			●	●	
<i>Mesocyclops aequatorialis</i>	●									
<i>Mesocyclops dussarti</i>			●							
<i>Mesocyclops ogunnus</i>		●			●			●	●	
<i>Mesocyclops sp.</i>						●				
<i>Thermocyclops decipiens</i>				●	●					
<i>Thermocyclops hyalinus</i>		●						●	●	
<i>Thermocyclops macracanthus</i>					●	●				
<i>Thermocyclops neglectus</i>	●	●						●	●	

Group / species	Lake Malawi	Lake Kariba	Lake Chivero	Cleveland Dam	Marondera	Nyanga	Lake Liambezi	Zambia (Kafue system)	Lake Bangweulu	Namibia (East Caprivi & Kavango R.
<i>Thermocyclops oblongatus</i>			•			•				
<i>Thermocyclops retroversus</i>					•					
<i>Thermocyclops tenuis</i>							•			
<i>Thermocyclops</i> sp.						•	•			•
<i>Macrocyclus albidus</i>	•	•					•	•		
<i>Microcyclus bicolor</i>							•	•		
<i>Microcyclus varicans</i>		•		•					•	
<i>Microcyclus rubelloides</i>									•	
<i>Eucyclops dubius</i>	•									
<i>Eucyclops euacanthus</i>							•			
<i>Eucyclops serrulatus</i>							•	•		
<i>Eucyclops stuhlmani</i>							•	•		
<i>Paracyclops fimbriatus</i>									•	
Cladocera: Sididae										
<i>Pseudosida szalayi</i>									•	
<i>Diaphanosoma excisum</i>	•	•	•	•	•	•	•	•	•	•
<i>Diaphanosoma sarsi</i>									•	
Cladocera: Daphniidae										
<i>Daphnia laevis</i>		•	•	•	•	•				
<i>Daphnia longispina</i>		•					•			
<i>Daphnia lumholtzi</i>	•	•	•							
<i>Daphnia pulex</i>			•	•	•	•	•			
<i>Daphnia rosea</i>						•				
<i>Daphnia</i> sp.					•	•				
<i>Ceriodaphnia dubia</i>		•	•	•			•			
<i>Ceriodaphnia quadrangula</i>					•	•				
<i>Ceriodaphnia reticulata</i>							•			•
<i>Ceriodaphnia</i> sp.	•									
<i>Simocephalus serrulatus</i>						•			•	
<i>Simocephalus vetulus</i>					•				•	
<i>Scapholeberis kingi</i>									•	
<i>Moina dubia</i>							•	•	•	
<i>Moina micrura</i>	•	•		•						•
<i>Moinadaphnia macleayi</i>							•			
Bosminidae										
<i>Bosmina longirostris</i>	•	•	•	•	•	•	•	•	•	
<i>Bosminopsis deitersi</i>		•					•			

Group / species	Lake Malawi	Lake Kariba	Lake Chivero	Cleveland Dam	Marondera	Nyanga	Lake Liambezi	Zambia (Kafue system)	Lake Bangweulu	Namibia (East Caprivi & Kavango R.
Macrothricidae										
<i>Ilyocryptus spinifer</i>								●	●	
<i>Ilyocryptus</i> sp.										
<i>Macrothrix triserialis</i>									●	
<i>Macrothrix</i> sp.				●			●			●
Chydoridae										
<i>Chydorus barroisi</i>									●	
<i>Chydorus eurynotus</i>									●	
<i>Chydorus globosus</i>									●	
<i>Chydorus hybridus</i>									●	
<i>Chydorus pubescens</i>									●	
<i>Chydorus sphaericus</i>									●	
<i>Chydorus</i> sp.			●	●		●	●			
<i>Acroperus harpae</i>									●	
<i>Alona affinis</i>								●		
<i>Alona guttata</i>								●	●	
<i>Alona karua</i>									●	
<i>Alona rectangula</i>								●	●	
<i>Alona</i> sp.							●			●
<i>Alonella excisa</i>									●	
<i>Oxyurella singalensis</i>									●	
<i>Camptocercus rectirostris</i>									●	
<i>Euryalona occidentalis</i>								●	●	
<i>Graptoleberis testudinaria</i>								●	●	
<i>Leydigia acanthrocercoides</i>									●	
<i>Pleuroxus chappuisi</i>								●	●	
<i>Pleuroxus denticulatus</i>								●	●	
<i>Pleuroxus</i> sp.							●			●
<i>Kurzia latissima</i>								●		
<i>Kurzia longirostris</i>									●	
Totals	11	16	11	12	15	14	10	33	44	11

Giant shrimps (*Macrobrachium* spp.) occur in the estuarine and lower reaches of rivers draining into the Indian Ocean and will occur in the Zambezi Delta as well as up the lower reaches of the Zambezi River itself. Monod (1980) gives a guide to the West African species but nothing about the East African ones could be located.

Subphylum Insecta

The insects are the largest and most diverse group of animals and their primary radiation has taken place in the terrestrial environment. Many insect orders have aquatic forms, almost all of which occur exclusively in inland waters. Most aquatic insects, with the exception of the Coleoptera (beetles) and Hemiptera (bugs), live in the water during their larval or nymphal stages and in the terrestrial environment as adults. In some cases the adult phase of the life cycle can be very short, lasting only a few hours or a few days, as in the Ephemeroptera and some dipteran groups like the chironomids. Because of their ability to fly adult insects have considerable powers of dispersion and most species would be expected to have a wide distribution. But too little is known about the distribution of aquatic insects in Africa to make any conclusions about their distribution and degree of endemism. Their ability to fly also allows insects to recolonize water bodies after drought and they are among the earliest invertebrates to appear in streams after the rains (Harrison 1966).

Most taxonomic studies deal with adult forms because larval ones frequently lack distinctive morphological characteristics. Many ecological papers therefore list insects to generic level only, while some of the methods for assessing water quality by means of biotic indices require identification to family only. Useful references at this level include Volume 2 of the *Flore et Faune Aquatiques de l'Afrique Sahelo-Soudanienne* (Durand & Lévêque 1981) and the SASS handbook (Thirion, Mocke & Woest 1995). A more detailed general work is Scholz & Holm (1985) which deals with all the orders of insects in southern Africa.

For accurate identifications it is necessary to refer to the primary taxonomic literature, which is often scattered and difficult to find. Some taxonomic papers, which contain data of interest to anyone working in the Zambezi Basin, are included in the discussion of each order, but the list is incomplete and can only be a general guide.

Order Collembola

The springtails are abundant in the terrestrial environment but still have to live in humid situations. Some are amphibious but only a few species live in water. Forge (1981a) gives a general outline of the group but nothing is known about aquatic collembola in the Zambezi Basin, although Magadza (1968) studied shoreline terrestrial collembola under *Salvinia* mats around Lake Kariba.

Order Plecoptera

Stoneflies are relatively uncommon, occurring mostly in small streams, and they have been neglected in the Zambezi Basin where most work has been carried out on lakes or reservoirs. Dejoux (1981) gives a general guide to African forms, while Hynes (1952a, 1952b) described the neoperlids of the Afrotropical region. Zwick (1976) is a general catalogue of Plecoptera that includes African species. No work from anywhere in the basin could be located.

Order Ephemeroptera

The mayflies are a very important group especially in running waters, but they have received little attention in the Zambezi Basin. General works on African mayflies include Demoulin (1970, 1981) and Peters & Edmunds (1964). The list of Ephemeroptera in the Natural History Museum of Zimbabwe includes species from many parts of the basin and is a useful introduction to this group (Gillies 1974). They, too, have been neglected in the basin because they are most abundant in small flowing streams and relatively rare in the standing waters that have been investigated most intensively. One exception is the widespread African mayfly *Povilla adusta*, which is one of the few to occur in standing waters. It has been recorded in Lake Kariba where it is an important food item for some fish species (Bowmaker 1973, Joubert 1975, Mitchell 1976a). It has been studied

extensively elsewhere in Africa (Hartland-Rowe 1953, 1955, 1957, 1958). In Lake Kariba *P. adusta* was able to colonise the drowned trees, where it made up from 77 to 93% of the insect biomass (McLachlan 1970b, Boon 1984).

Order Odonata

The dragonflies and damselflies are well-known aquatic species because the adults are relatively large, brightly-coloured, and conspicuous diurnal forms. Their taxonomy is relatively well known and, thanks to the work of Eliot Pinhey, it is possible to make lists for various parts of the Zambezi Basin. This work has been reviewed separately (see Chapter 9).

Order Orthoptera

The grasshoppers and locusts are almost exclusively terrestrial and it is not clear if any aquatic species occur in Africa. The group Tetrigidae will take to water and swim below the surface to escape their enemies. The South American species *Paulinia acuminata* is of some interest because it was brought to the region as a biological control agent to control the aquatic weed *Salvinia molesta*. It is a small, flightless, polymorphic species (Meyer 1979) that lives on and underneath *Salvinia* plants, swimming well under water when necessary. It now occurs in the Chobe-Linyanti system, and in Lakes Kariba and Cabora Bassa. Its efficacy as a biological control agent is debatable; Mitchell & Rose (1979) suggested that it did control the weed on Lake Kariba but Chisholm (1979) and Marshall & Junor (1981) were more sceptical.

Order Hemiptera

The waterbugs are widespread and abundant in most aquatic habitats, especially small streams and pools, including seasonal ones. They include well-known forms like the pond-skaters (Gerridae), backswimmers (Notonectidae), water scorpions (Ranatridae), Belastomatidae and Coixidae. There is a large literature on the group, but little from the Zambezi Basin. Worldwide reviews of some important groups include the work of Hungerford (1933), Hungerford & Matsuda (1960) and Andersen (1995) while general works on African hemipterans include de Sallier Dupin (1976) and Dethier (1981). Drake (1963) described some new species from central Africa (which may include parts of the Zambezi Basin) while Hutchinson (1933) considered their zoogeography in Africa. The only known ecological study from anywhere in the basin dealt with species found in temporary pools in the Hwange National Park (Weir, 1966).

Order Neuroptera

The lacewings and their allies are typically terrestrial with only a few aquatic species. The papers by Elouard (1981) and Tjeder (1957) may be useful to workers in the Zambezi Basin, while Smithers (1957) described two species from Zimbabwe.

Order Trichoptera

Caddisflies are amongst the most important members of stream communities and are well known in South Africa, primarily through the work of K.M.F. Scott. She produced an extensive bibliography on African trichopterans (Scott & Scott 1969) and a general overview of the group in southern Africa (Scott 1986). A general account of the group is given in Marlier (1981) while the papers by Scott (1970, 1976) are of interest to workers in the basin. One of the few investigations from anywhere in the Zambezi Basin is that of Boon (1986) who described net spinning in *Amphipsyche senegalensis* in Lake Kariba. This species normally inhabits running water but it is likely that water movements around the trees enabled it to survive in the lake.

Order Coleoptera

The beetles are the largest order of animals and are an extraordinarily diverse, but predominantly terrestrial group. As might be expected, there are a number of aquatic families that are most commonly found in streams, ponds and seasonal waters, rarely in large lakes or rivers. They are unusual amongst aquatic insects in that both larval and adult forms are aquatic, although the adults can survive out of water and fly readily. The most important families are the Dytiscidae (giant water beetles) and the Gyrinidae (whirligig beetles) and these have been investigated in most detail. Forge (1981b) gives a useful general introduction to African water beetles, while Brinck (1955a, 1955b, 1955c) dealt with African gyrenids, and with the gyrenids of Malawi and Mozambique (Brinck 1960a, 1960b) which are relevant to the Zambezi Basin.

The Dytiscidae of southern Africa were dealt with by Omer-Cooper who published a series of ten papers on dytiscids from Malawi and Zimbabwe (eight of them summarised in Omer-Cooper 1965a, the others in Omer-Cooper 1965b, 1967). According to this work, there were some 27 dytiscid genera in the basin with about 142 species. However, there are 150 species of Dytiscidae in Malawi alone according to Dudley (pers. comm.). The most diverse genera were *Hydrovatus* (19 species), *Cybister* (19 species) and *Laccophilus* (18 species). These estimates are probably incorrect now because further dytiscid collections have been made. They include some from South Africa and Zimbabwe (Bertrand & Legros 1967) and Namibia (Hebauer 1995). Bistrom (1996) reviewed the dytiscid genus *Hydrovatus* as well as naming a new species and giving distributional records of others in Namibia (Bistrom 1995). The dytiscids of parts of the Zambezi Basin, at least, seem therefore to be relatively well known.

Few of the smaller beetle families have been reviewed on a regional or continental scale, with the exception of a review of the Dryopidae of the Afrotropical region (Bertrand 1967). Finally, an important series of papers deals with the larval stages of the aquatic beetles of the Afrotropical region (Bertrand 1961, 1962, 1963, 1964, 1965, 1966, 1969a, 1969b). These would be of considerable value to anyone working on benthic fauna in small pools where beetles are likely to be abundant.

Of some interest are the weevils (family Curculionidae) that have been introduced into various countries in the basin to control alien aquatic weeds. They are not themselves aquatic since their larvae live in the plants and not in the water, but they are of importance in ecological terms through their possible impact on the floating weeds. One of the earliest to be imported from South America was *Cyrtobagous singularis* to control *Salvinia molesta* (May & Sands 1986, Sands & Kassulke 1986). This species is well established in the Caprivi Strip (Kwando and Chobe systems) (Schlettwein 1985) and northern Botswana (Proctor 1984). *Neohydronomus affinis* has been used to control water lettuce, *Pistia stratiotes*, in Zimbabwe and Botswana (Chikwenhere & Forno 1991, Chikwenhere 1994a). Other South American weevils, *Neochetina brucei* and *N. eichhorniae*, have been used to control water hyacinth, *Eichhornia crassipes*, with considerable success in some areas like Lake Chivero (Chikwenhere 1994b). The insect has been introduced onto Lake Kariba to control the outbreak of water hyacinth there and it is likely to spread to Lake Cabora Bassa and other parts of the Zambezi.

Order Diptera

Many dipteran families have aquatic larval stages, among them the Culicidae (mosquitoes), Simuliidae (blackflies) and Ceratopogonidae (biting midges) that are vectors of human and animal diseases. Other aquatic dipterans include the Tabanidae (horseflies), Chironomidae (non-biting midges) and Chaoboridae (ghost midges), which are all of considerable ecological importance. In

all aquatic dipteran families, only the larvae and pupae live in water; the adults emerge to a terrestrial existence. General comments on the biogeography of Diptera in southern Africa are given in Bowden (1978), while Elouard (1982) gives a general introduction to the order and some of its less important families. An important source, which gives keys to families, subfamilies and genera of all dipteran families, is Crosskey (1980) and it has been used to estimate the number of species in the principal families of aquatic diptera (Table 11.4). The estimates are almost certainly too low because little collecting has been done in many areas and the distribution of most species is still poorly known. It is likely that many new species have been described since this catalogue was published in 1980. Malawi has approximately 62 species of mosquitoes, 23 species of blackflies, 116 species of horseflies and 31 species of non-biting midges (C. Dudley, pers. comm.).

The craneflies (Tipulidae) are the largest family in the Diptera but they have generally been little studied. Their biology is poorly known, especially in Africa and there seems to have been little work done in the Zambezi Basin (which may explain why there are so few species that have been recorded from it; Table 11.4). The only relevant paper seems to be that of Alexander (1963).

The psychodids are a small family with only about 100 Afrotropical species (Table 11.4), although this number is likely to increase with further collecting. The larvae live in a variety of aquatic habitats, including foul ones like the biological filters of sewage works. They can become very abundant in these situations and play an important part in breaking down the organic matter in sewage. Nothing seems to be known about their ecology anywhere in Africa.

Table 11.4. The approximate number of aquatic Diptera in the Afrotropical region, and in the Zambezi Basin. Estimated from data in Crosskey (1980). Zambezi Basin records are based on species recorded from Angola, Malawi, Mozambique, Zambia and Zimbabwe.

	Afrotropical Region		Zambezi Basin	
	Genera	Species	Genera	Species
Tipulidae	55	1321	33	97
Psychodidae*	20	100	8	12
Culicidae	13	605	9	137
Simuliidae	3	165	3	31
Chaoboridae	2	11	1	5
Chironomidae	97	372	57	123
Ceratopogonidae	35	625	21	75
Tabanidae	30	722	21	268
Total	255	3921	153	748

* excludes the subfamily Phlebotominae, the larvae of which are not aquatic.

Mosquitoes (Culicidae) are particularly important in Africa because they are vectors of malaria. Major efforts to control the disease have been made for almost a century and there is now a huge literature on the physiology and behaviour of adult mosquitoes, as well as on disease transmission and control efforts. Much less is known about their biology and ecology during their larval and pupal phases in the aquatic medium. Hopkins (1952) and Rickenbach (1981) give a general

introduction to African mosquitoes, while Khamala (1968) illustrates East African species. Jupp (1996) published a similar volume for southern Africa and it should be valuable for anyone working in the Zambezi Basin. The Anophelinae were reviewed by Gillies & de Meillon (1969) and the zoogeography of *Aedes* is discussed by Reinert (1970). An extensive checklist, with distribution maps, of Zimbabwean mosquitoes was published by Reid & Woods (1957), but this is probably out of date now if only because of the discovery that some species are actually species complexes.

These species complexes involve several morphologically identical species that can only be separated by cytological or biochemical means. The best known is the *Anopheles gambiae* complex, which has been studied in detail because one of the four species that make up the complex is a vector of malaria (Green 1970, 1972, Mahon, Green & Hunt 1976). Attempts to find methods to separate the species by morphological techniques have not been particularly successful (Zahar, Hills & Davidson 1970). The extent to which species complexes occur among species that do not transmit malaria is unknown, although there is evidence that they exist among *Aedes aegyptii*, the vector of yellow fever (Paterson, Green & Mahon 1976).

Second in importance to mosquitoes in Africa is the family Simuliidae (blackflies). In west and central Africa they are important vectors of onchocerciasis (river blindness), while in South Africa they are important pests of livestock, having become abundant after river flow patterns changed through regulation. Neither of these problems is particularly serious in the Zambezi Basin where much less attention has been paid to simuliids, in contrast to those in other parts of the continent. Important general guides to the African Simuliidae include Freeman & de Meillon (1953), Crosskey (1962, 1969) and Phillipon (1981). Palmer (1991) produced a regional checklist for southern Africa.

Other biting flies also have aquatic larval forms. The ceratopogonids are small biting midges, of which the best known is the genus *Culicoides* that, apart from their nuisance value, transmit various human and animal diseases. A general guide to African ceratopogonids is provided by Cornet (1981) while more detailed information is available in a series of 12 papers by de Meillon & Wirth (the most recent is de Meillon & Wirth (1991) and contains bibliographic information on the others). Very little is known of their larval biology and ecology, i.e. during their aquatic stage, in the basin. Braverman (1978) described some of the characteristics of their breeding sites around Harare, Zimbabwe, as well as some aspects of their biology and abundance (Braverman 1977, Braverman & Phelps 1981).

Another large and important group of biting flies with aquatic larvae is the Tabanidae (horseflies), which are significant mostly because of their nuisance value to domestic animals, although they do transmit some diseases. General guides to the tabanids of Africa are available in Oldroyd (1952, 1954, 1957) and Taufflieb (1981), while Travassos Santos Dias (1988) listed species from southern Africa. Goodier (1967) published a list of 88 species of Zimbabwean horseflies, although not all of them may have occurred in the Zambezi Basin, while Clarke (1968) and Phelps & Vale (1975) investigated their seasonal occurrence in Zambia and Zimbabwe, respectively.

An important family of non-biting midges is the Chaoboridae, whose larvae are important components of both the benthos (early instars) and zooplankton (late instars) (Mitchell 1976b). It is a relatively small family with perhaps only four species occurring in the Zambezi Basin; *Chaoborus edulis* (the most widespread and the only one apparently in Lake Malawi), *C. anomalus*, *C. ceratopogones* and *C. pallidipes* (Mitchell 1975, 1988, Irvine 1995b). Chaoborids are especially important in Lake Malawi, where dense swarms of adult lakeflies rising in a narrow column from the lake's surface are a visually striking feature. The FAO fishery expansion project concluded that

Chaoborus (the larvae are predaceous) competed for plankton resources with pelagic fish, which accounted for the low pelagic productivity of the lake (Turner 1982). It is likely that the quantity of zooplankton eaten by *Chaoborus* was overestimated and Irvine (1995b, 1997) estimated that it consumed 10-20% of the crustacean zooplankton production. The impact of this is probably reduced by the fact that *Chaoborus* is itself an important resource for many fish species living in the lake (Allison *et al.* 1995, Thompson & Irvine 1997).

Chaoborus was abundant in Lake Kariba during its early years when it was the major open-water predator on zooplankton (Bowmaker 1973, Mitchell 1975, 1988). This situation changed after the kapenta *Limnothrissa miodon* was introduced in 1967-68, which quickly reduced the population of *Chaoborus* in the lake (Marshall 1991). It is certainly absent from the zooplankton in open water but may still occur in protected shallow water areas, as other larger planktonic species do (Green 1985). Otherwise *Chaoborus* can only be expected to occur in the lake if it is carried there as part of the invertebrate drift in the inflowing rivers (Mills 1976). The same situation occurs in Lake Cabora Bassa where *Chaoborus* is rarely recorded (Gliwicz 1984). Elsewhere in the Zambezi Basin, chaoborids have been reported from a number of localities around Harare and in the Zambezi valley (Mitchell 1988).

The largest family of non-biting midges is the Chironomidae and they are widespread in all water bodies. Dejoux (1981) gives a good general guide to the family, while the main taxonomic study of African chironomids is Freeman (1955, 1956, 1957, 1958), although Cranston & Edward (1998) review the African genus *Afrochilus* and discuss the phylogeny of the subfamily Podonomonae. A review of the genus *Dicrotendipes*, which is widespread in Africa and known from both lakes Kariba and Chivero, is given in Efler (1988). Descriptions of larvae and pupae from Lake Kariba (McLachlan 1969a) and Malawi (McLachlan 1971) are of interest as they are among the few papers on the juvenile stages of these insects in Africa. He also provides a cautionary note on the use of prolegs, anal papillae and 'gills' in larval taxonomy, since these structures vary in relation to the conductivity of the water (McLachlan 1976). Despite the extensive work that has been done on African chironomids, new forms continue to be discovered, e.g. the records of *Doithrix* and *Georthoclades*, the first from the Afrotropical region, which came from the Zambezi Basin (Seuther & Andersen 1996).

Some chironomids are able to live in the small ephemeral rock pools that commonly occur in many parts of the basin, and fill up after rainfall (McLachlan 1981, 1983, 1988, McLachlan & Cantrell 1980). One of them, *Polypedilum vanderplanki*, is a cryptobiotic species and can survive the dry season as a larva through an extraordinary ability to survive for many years in an almost completely desiccated state (cryptobiotic). Although these rock pools may only last for a few days they amount to permanent habitats for this species. The other rock pool species, *Chironomus imicola*, is unable to survive like this and must seek new pools as an adult. In contrast to *P. vanderplanki* it has a very short life cycle, averaging 12.2 days from egg to adult.

Much of the interest in chironomids stems from their importance as benthic animals, where they have an important function in cycling detritus and as food for fish. Species in the subfamily Chironominae are also able to survive in polluted situations where oxygen is deficient because the blood of the larvae has an oxygen-transporting substance, which gives them a bright red colour (hence the name "blood worms"). Most of the work on chironomids in the Zambezi comes from Lake Kariba, as part of McLachlan's (1974) investigation into the evolution of lake ecosystems. He was particularly interested in the effects of water level fluctuations (McLachlan 1970a) and the impact of aquatic macrophytes (McLachlan 1969b) on chironomid communities. Chironomids were

also fairly numerous (about 11% of the biomass) on the drowned trees in the early years after the lake was created (McLachlan 1970b), but they had decreased in importance (to only 0.001% of the biomass) by the 1980s (Boon 1984). The relationship between chironomids and sediments was investigated in the field (McLachlan & McLachlan 1971) and in the laboratory (McLachlan 1969c).

Chironomids were also investigated in Lake Chivero in an attempt to determine the effect of eutrophication (Marshall 1978, 1982). Their abundance here was strongly seasonal and related to fluctuations in water level; as at Kariba the chironomids increased in numbers as the lake level rose and nutrients were released from the exposed shore. But in Lake Chivero, chironomid larvae were restricted to the first few metres, with the deeper sediments being dominated by oligochaetes. There was little change in their abundance over thirty years (Marshall 1995) despite the increasing severity of pollution in the lake. Few other data are available on benthos from anywhere in the basin, apart from some brief comments in Seaman *et al.* (1978) who noted that chironomids were among the dominant benthic species in Lake Liambezi.

Finally, benthic insects, especially chironomids, have been investigated because of their importance as fish food. Work on fish feeding has been centred on Lake Kariba where Mitchell (1976a) and Joubert (1976) both recorded a wide range of insects in the diet of most fish species. Even the almost exclusively piscivorous tigerfish, *Hydrocynus vittatus*, fed on invertebrates during its juvenile stages (Kenmuir 1975). Similarly, in Lake Chivero Munro (1967) and Marshall & van der Heiden (1977) found that almost all fish species fed on benthic insects and other invertebrates. This emphasises their importance in aquatic systems.

11.3 CONSERVATION

11.3.1 Conservation of invertebrates

Little importance has been attached to the conservation of invertebrates in Africa and it is probably true to say that most people on the continent are quite indifferent to the idea. Indeed, most would probably prefer to eliminate them, supporting campaigns against snails, mosquitoes or blackflies without any regard for the consequences to other species. This is a shortsighted attitude, of course, since invertebrates are vital for the functioning of ecosystems, processing organic matter and nutrients, as food for other animals, and as biological control agents for a variety of pest species. This view is reflected in the relative paucity of papers dealing with the conservation of aquatic invertebrates. Of the Zambezi Basin countries, only Namibia has made any attempt to draw up a checklist of species and articulate a conservation policy (Curtis *et al.* 1998).

Aquatic systems throughout the basin are subject to various human activities that affect their biota in one way or another. Of particular concern is the use of pesticides to control mosquitoes (vectors of malaria), tsetse flies (nagana) or snails (bilharzia) because of their impact on non-target species. Very little is known about the impact of these operations on aquatic invertebrates apart from an evaluation of the effect of a molluscicide on stream fauna (Harrison & Mason 1967) and some work on the impact of endosulfan, used to control tsetse, in the Okavango Delta (Russel-Smith 1976, Russel-Smith & Ruckert 1981).

Other activities that have an impact on aquatic systems include agriculture and land clearance, pollution and siltation, but very little is known about their effect on aquatic invertebrates. Organic pollution in streams around Harare, as elsewhere in the world, caused a loss of insect species with only chironomids being able to survive in the most affected areas (Marshall 1972). Even amongst

the chironomids, only *Chironomus* is able to resist severe pollution, while other genera, like *Procladius*, *Tanytus*, *Pentaneura*, *Dicrotendipes* and *Nilodorum*, were dominant in less severely affected areas.

Little attention has been paid to the introduction of alien invertebrate species, apart from some brought in as biological control agents and others for aquaculture purposes. Many insect species have remarkable powers of dispersal because of their powers of flight and the ability to use the winds to carry them long distances. The increase in air travel has assisted many species, especially mosquitoes, to spread, which explains how species like *Aedes aegyptii* and *Culex pipiens* reached southern Africa (de Moor 1992). Both are potential disease vectors and their appearance is a cause for concern.

At present, temporary waters are the most vulnerable ecosystems in the region. The invertebrate species that live in them are well adapted to arid conditions and can survive drought but, because many of them are relatively large, they cannot survive fish predation. The introduction of fish into these pools, which often follows when they become permanent after water is pumped into them, can have a serious impact on the invertebrate fauna. Such a situation occurred in the Hwange National Park where some seasonal pools became permanent when water was pumped into them to supply game animals during the dry season. The pools were stocked with Catfish, *Clarias gariepinus* and the diversity of insects (mostly Hemiptera) and other invertebrates was greatly reduced (Weir 1972). In this case, the consequences were perhaps not serious since none of the species were endemic and there are numerous other seasonal pans in the park which cannot support fish. But some seasonal pools support endemic crustacean species and these populations are at risk if fish are introduced into these pools. An example of this danger is illustrated by the possible extermination of hitherto undescribed and endemic crustacea in Rhino Ridge Pool in South Africa that followed the introduction of fish into it (Martens & de Moor 1995). Ironically, this occurred in a nature reserve where managers were attempting to improve a bird observatory.

11.3.2 The present state of knowledge

The destruction of the crustaceans in the Rhino Ridge Pool came about through ignorance. It was done by conservationists for the best of motives – to improve and develop a bird observatory and educational facility – but without any realisation that unique species may have existed. This reflects the need for a greater understanding of aquatic invertebrates and their importance. This understanding will not be achieved without investment in basic taxonomy and ecological studies. At present, most invertebrate taxonomists are based in Europe and North America, with very few in South Africa, and few African countries have the resources to employ taxonomists, give them the special training they need and maintain the museum collections that have to be built up. Unfortunately donor funding for biodiversity is increasingly linked to human social interests and the culture of utilizing resources (Attwell & Cotterill, in press); funding for naming and counting species is increasingly difficult to obtain.

One exception to this is the increasing use of aquatic invertebrates to monitor water quality and programmes to accomplish this are well developed in some countries, like Australia (Chapman 1995) and South Africa (Chutter 1998). Little has been done in the Zambezi Basin, apart from some work in streams around Harare (Gratwicke, in press), but it is hoped that more will follow. Projects like this should stimulate an interest in invertebrates and bring their importance in aquatic systems to a wider range of people.

11.4 CONCLUSIONS AND RECOMMENDATIONS

The knowledge of aquatic invertebrates is generally rather sparse in most parts of the Zambezi basin. It is difficult for field workers to do much on them since they can usually only be identified by people with specialist knowledge and access to appropriate microscopes. The scattered nature of the literature and the lack of good field guides is another impediment to understanding. Also, while funding may become available for fisheries investigations, which have an obvious economic justification, it is rare for projects in invertebrate biology to be funded adequately (an obvious exception is those species of medical or veterinary importance). These comments apply to the basin as a whole, but there are some areas where more detailed information on some invertebrate groups is available.

11.4.1 Summary of knowledge by area

A preliminary assessment of the state of knowledge of aquatic invertebrates from the various sections of the Zambezi Basin is given in Table 11.5, and briefly outlined below.

Upper Zambezi

As in most of the basin, invertebrates have been studied only in localized areas. The most important of these is the Kavango and Chobe systems in Namibia, from which collections have been made. While attempts have been made to list all the aquatic macro-invertebrates known from Namibia, relatively little is known of their biology.

Middle Zambezi

Data are available from some parts of the Middle Zambezi system. Lakes Kariba and Chivero have been studied in some detail, with data available for the benthos (notably molluscs, Chironomidae (Diptera) and oligochaetes), and the planktonic microcrustacea and rotifers. The planktonic crustacea of Lake Cabora Bassa have also been investigated in some detail but nothing else is known about the invertebrates of this lake. Smaller reservoirs have been investigated to a lesser extent but the detailed checklists of rotifers from Zimbabwe are a noteworthy contribution. River systems have been largely neglected, apart from a few studies in stream ecology in Zimbabwe and some data from the Kafue River, collected a long time ago.

Lower Zambezi

Almost nothing has been published on invertebrates of the Lower Zambezi, which remains a priority area for further investigations.

Lake Malawi

The aquatic invertebrate fauna of Malawi seems to be quite well known and lists of species have apparently been prepared, although they are not readily available (C. Dudley, pers. comm.). The lake itself is of special importance since it has a number of endemic species amongst the molluscs and the crustacea (and probably other groups, too).

11.4.2 Use of aquatic invertebrates for monitoring

Knowledge of aquatic invertebrates is likely to become increasingly necessary in future for anyone involved in managing water quality. It is well known that communities of aquatic invertebrates respond to changes in the physical and chemical environment in which they live. In many parts of the world attempts have been made to use this fact to detect water pollution and to manage water quality. A simple method of determining the state of the aquatic invertebrate community, and use

[Back to Contents](#)**Table 11.5.** State of knowledge about the major invertebrate groups in the Zambezi Basin (1 = none/virtually none; 2 = very poor to poor; 3 = moderate to good).

Group	Upper Zambezi			Middle Zambezi			Lower Zambezi			Lake Malawi		
	Taxonomy	Distribution	Ecology	Taxonomy	Distribution	Ecology	Taxonomy	Distribution	Ecology	Taxonomy	Distribution	Ecology
Protozoa ¹	1	1	1	1	1	1	1	1	1	1	1	1
Porifera ²	2	1	1	2	1	1	1	1	1	2	1	1
Cnidaria ³	2	1	2	2	1	2	2	1	2	2	2	2
Turbellaria	1	1	1	1	1	1	1	1	1	1	1	1
Rotifera ⁴	2	3	1	3	3	2	2	1	1	1	2	1
Nematodes	1	1	1	1	1	1	1	1	1	1	1	1
Oligochaetes ⁵	2	3	1	2	2	3	1	1	1	2	2	1
Crustacea ⁶	3	3	1	3	3	3	1	1	1	3	3	3
Chelicerata	1	1	1	1	1	1	1	1	1	1	1	1
Insecta ⁷												
a) Ephemeroptera ⁸	2	1	1	2	1	1	1	1	1	2	1	1
b) Odonata ⁹	3	3	1	3	3	1	3	2	1	3	2	1
c) Coleoptera ¹⁰	2	2	1	2	2	1	2	1	1	2	2	1
d) Diptera ¹¹	2	2	1	3	3	2	1	1	1	2	3	1
Mollusca	3	3	1	3	3	2	3	2	1	3	3	1

Notes:

1. Ciliates are important pelagic species in Lakes Tanganyika and Kivu, but not apparently in Lake Malawi or anywhere else in the Zambezi Basin. This seems to be linked to the impact of planktivorous clupeids; in Lake Kivu the ciliates only appeared after the larger zooplankton were eliminated by *Limnothrissa*.
2. Records of sponges are available from the Okavango and Chobe systems in Namibia (UZ), Lake Kariba and Mwenje Dam (MZ), and from Lake Malawi from which several species have been described. Nothing is known of their ecology.
3. The taxonomy of cnidarians is well known as far as medusae are concerned since there is only one species (sometimes thought to be two), but less in known about polyps. The only ecological study of jellyfish comes from Lake Kariba.
4. The rotifers are especially well-known in the Middle Zambezi, thanks to the work of Green in Africa in general, and Lake Kariba and other reservoirs in particular. Very little is known about their ecology.
5. The oligochaetes have been studied intensively in Lake Chivero (MZ), from which some ecological data are available. Other collections have been made in the Okavango system (UZ), Lake Kariba (MZ) and Lake Malawi.
6. The planktonic crustacea are generally well known in all systems except perhaps the Lower Zambezi. Their ecology has been studied in considerable detail in Lakes Kariba and Cabora Bassa (MZ) and Lake Malawi. Less detailed studies are available from a number of reservoirs in Zimbabwe (MZ) and Lake Liambezi (UZ).
7. The smaller insect orders have not been studied intensively in the basin, where most work has concentrated on the larger orders like the Diptera.
8. The taxonomy of southern African Ephemeroptera is quite well known, thanks to the work of K.M.F. Scott, but their ecology has not been studied in much detail anywhere in the basin.
9. The Odonata are well known from a taxonomic point of view – perhaps more so than any other insect order – through the work of Elliot Pinhey. The same cannot be said about their ecology, which has been little studied anywhere in the basin.
10. Some coleopteran groups, like the family Dytiscidae, are quite well known but their ecology is poorly understood.
11. Dipteran groups that are of medical or veterinary importance are well known, as are some others like the Chironomidae, which have been studied extensively in Lake Kariba.
12. Of all the invertebrate groups, the molluscs are best known taxonomically because there are relatively few species (compared to the insects) and their medical importance requires accurate identification. Their ecology has been studied in most detail in Lake Kariba and parts of Zambia and Zimbabwe (MZ), partly in relation to bilharzia control. Lake Malawi has a large mollusc fauna, with a number of endemic species, which has not been thoroughly studied.

it as an index of water quality, has been developed in South Africa. It has been termed SASS (South African Scoring System).

The system involves collecting a sample of invertebrates from a stream or river using a standardised net and following defined methods (Chutter 1998). The invertebrates collected are tipped into a tray and the types recorded. It is generally only necessary to record each type to family level, which is usually possible with standard guides. Each family is given a number from 1 to 15, which reflects its sensitivity to changes in water quality; the most tolerant families are ranked 1 and the least tolerant 15. The SASS score is the sum of the numbers against each recorded taxon, the ASPT or average score per taxon is the SASS score divided by the number of taxa. Unaltered water will have high SASS or ASPT scores while very low scores will be recorded in severely polluted systems.

This system has been very successful in South Africa in assessing water quality over extensive catchment areas (Chutter 1998) and has been successfully adapted for use in Zimbabwe (Gratwicke, in press). The SASS method is presently most suited to riffles in streams and small rivers, but it can probably be adapted for use in larger rivers and floodplain systems. Its advantage is its simplicity; the only equipment needed is a hand net and some basins, buckets, and so on, and most invertebrates can easily be identified to family level. Furthermore, the invertebrate community is continuously exposed to pollutants and therefore responds to sporadic discharges that are not easily detected by chemical analysis.

Biomonitoring of this kind could allow a network of pollution monitoring stations to be established throughout the Zambezi basin, with a rather higher density in areas where pollution problems are known to exist. The costs of running such a programme are generally within the means of most government departments within the region although donor funding might be needed to train personnel, provide some equipment, and so on.

11.4.3 Recommendations

Conservation agencies should make more effort to recognize the importance of invertebrates. They are by far the most numerous animals in aquatic systems, and also the least known. They represent the largest gap in our understanding of biodiversity, and this alone warrants more study. Most of them have no obvious economic or social value so this means that a fundamental change in the approach taken by most agencies, who will have to recognize that the study of biodiversity is intrinsically important.

Some of the steps that might be taken include:

- (a) Scientists and specialists could be asked to summarize all the available data on particular invertebrate groups. This would have to involve a review of the primary taxonomic literature, an evaluation of all specimens available in museums throughout the world, and an opportunity to locate the grey literature available in countries of the region. This would obviously be a costly business and could not be done without a significant commitment of funds over a long period.
 - (b) At the same time museum resources in the basin need to be strengthened. This would have to include funds for the appointment and training of new curators, as well as operating funds so that they can establish and expand collections, and to publish their work. It has to be accepted that invertebrate identification requires trained specialists who require lifelong practice before becoming fully conversant with their special groups. This requires long-term financing.
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- (c) Some short-term projects that would stimulate interest in invertebrates could also be established. One example might be to establish a basinwide programme to assess water quality using the SASS system, with appropriate modifications. Such a programme would obviously need a co-ordinator, but local people could be trained to sample in their own areas and the requirements for equipment are relatively small.

11.5 REFERENCES

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