ZOOPLANKTON OF THE OKAVANGO DELTA AND ASSOCIATED BASINS IN BOTSWANA

by

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Chapter 1

INTRODUCTION

The United Nations (UN) appropriately assigned the theme ‘Water for Life’ to the 2005 to 2015 International Decade for Action. The primary goal was to encourage countries to work towards accomplishing the water-related goals of the 2000 Millennium Declaration and of Agenda 21, part of which was to halve the number of people lacking access to safe drinking water and sanitation (UN 2016a). Thereafter, in October 2010, the United Nations General Assembly declared the period 2011 to 2020 as ‘the United Nations Decade on Biodiversity’, the goal of which is to contribute to the implementation of the Strategic Plan for Biodiversity (UN 2016b). This comes at a time when the biodiversity of freshwater resources are facing unparalleled and mounting threats from human activities.

Although freshwater habitats cover a mere 0.8% of the earth's surface and contain only 0.01% of the global water supply (Dudgeon *et al.* 2006), it supports more than 125,000 species, which is approximately 9.5% of all species described on the planet (Strayer & Dudgeon 2010). Rivers and wetlands are probably the most threatened of all ecosystems, as biodiversity declines in these environments exceed that of the most endangered terrestrial ecosystems by far (Dudgeon *et al.* 2006). Despite their obvious importance and the serious threats they face, freshwater ecosystems remain poorly understood and inadequately represented in biodiversity assessments (Amis *et al*. 2007) and our knowledge of the total species diversity is ominously incomplete. This is particularly true for invertebrates and microbes (Dudgeon *et al.* 2006).

In southern Africa, a great deal remains to be explored about the biogeography, biodiversity and biological integrity of aquatic ecosystems (Day 2003). Day (2003) pointed out that a large number of aquatic species, particularly in small, ephemeral habitats, may already have, and continue to, become extinct and that it is crucial to conduct surveys of biodiversity and the state of aquatic ecosystems soon enough for future extinctions to be prevented or at least recorded.

As secondary producers and primary consumers, zooplankton play a crucial role in any aquatic ecosystem. This collective of aquatic organisms is important in structuring phytoplankton communities and in facilitating energy flow to higher trophic levels in all aquatic environments (Barnett *et al.* 2007). Currently, studies conducted on freshwater zooplankton in southern Africa are few and a lot of focus is being placed on marine and estuarine species, while the freshwater species have largely been neglected. Furthermore, the majority of research in freshwater systems has been conducted in unnatural impoundments, such as dams, while natural ephemeral systems have been overlooked.

Southern Africa is scattered with ephemeral water sources, as throughout much of the area rainfall is seasonal, extremely unpredictable and is exceeded by evaporation rates. This results in much of the area suffering from serious water deficits and periodic droughts most of the time. Large areas of southern Africa receive less than 1,000 mm of rain annually and runoff is less than 20% of the rainfall (Thomas & Shaw 1991; Pallet 1997). This means that more than two thirds of the rainfall input is lost to evaporation and transpiration. Furthermore, climate variability and periods of drought and flooding are normal events in the hydrological context of southern Africa and a number of natural cycles affect the rivers of the region (McCarthy *et al*. 2000).

One such river system which is continually affected by periods of drought and flooding is the Okavango River System. Spanning three countries, this river starts its journey in the highlands of Angola, after which it enters the Caprivi Strip in Namibia, where it flows as a single river, before spreading across the sands of the Kalahari Desert in Botswana. The delta is maintained by the annual pulse flooding of the Okavango River (from the highlands of central Angola) creating one of the world's largest inland wetland systems. The Okavango Delta contains unique habitats with a remarkably high beta diversity and, as such, is one of the World Wildlife Fund's (WWF) top 200 eco-regions of global importance (Hughes *et al*. 2010) and one of the world's largest Ramsar sites (wetlands which are considered to be of international importance and are designated under the Ramsar Convention). In 2014 it was also listed as the 1000th UNESCO World Heritage Site.

The Kalahari Desert encompasses most of the land-locked country of Botswana, in which the Okavango Delta, one of the least developed river basins in Africa, is situated. Sand dominates the landscape and there is almost no surface water, except after rain, which is erratic in the area. Many of the aquatic systems in Botswana are ephemeral, some containing water for short periods annually, while others dry up for as long as 40 years, before being inundated again. Hence, for the people of Botswana, the Okavango Delta and its associated basins are of critical importance to their livelihoods and well-being.

Unsurprisingly, the Okavango Delta has been listed as one of seven globally important wetlands (Junk *et al.* 2006). In 2006 a special edition of the journal *Aquatic Sciences* was published in which the species diversity data of these wetlands was compared. This followed the realisation that freshwater lake, river and wetland environments were largely overlooked in biodiversity studies, despite the rapid rate of species decline and loss and degradation of wetland habitats (Junk *et al.* 2006). Ramberg *et al*. (2006) took on the daunting task of summarising available data on the species diversity of the Okavango Delta. Their summary of aquatic invertebrates is patchy and incomplete and they stated that: “The data on invertebrate species in the Okavango Delta is far from comprehensive and many taxonomic groups are too difficult to collect, or nobody has tried to sample them, while some are taxonomically not well-known or there are no taxonomists able to identify them”. If anything, this paper indicated the pressing need for limnological studies in the Okavango Delta. This is even more so for basins associated with the Okavango Delta, such as the Thamalakane River, Lake Ngami, the Boteti River, Lake Xau and the Nata River, the majority of which have never been sampled for zooplankton before.

The lack of limnological studies in the Okavango’s associated basins has been due to a prolonged period of drought, which left many of these basins bone dry for between 20 and 40 years. The rivers and lakes of northern Botswana are all really one system as they are connected at various times and intervals and although the Okavango is a permanent system, the above-mentioned basins associated with it are ephemeral. During the early stages of the present study, the catchment of the Okavango River, in the highlands of Angola, experienced exceptionally high rainfall which resulted in the flooding of the Okavango Delta. For the first time in decades enough outflow left the delta to fill its associated basins, which rapidly stabilised and became highly productive, warranting the reference as instant ecosystems. This provided a perfect, snapshot opportunity to not only sample zooplankton species from the Okavango Delta, but also throughout its newly inundated associated basins. Against this background, the present study was undertaken to:

- obtain specimens of aquatic micro-invertebrates (while the opportunity presented itself) from an area lacking zooplankton data and which may or may not be inundated again in decades,
- correctly identify species of Rotifera and micro-Crustacea up to species level (using available literature), where possible, and thereby produce a comprehensive list of zooplankton taxa with correct species identifications,
- create a photographic record of organisms present in the Okavango Delta and its associated basins,
- map the distribution of individual species within the study area making use of Geographic Information Systems (GIS).

This study serves as a continuation of the author's research for her Masters dissertation (West 2010) which examined the conservation condition and, more specifically, the water quality of the Unprotected Okavango Delta (as water quality was continually recorded at all sites during the present study). It also builds on the previous study by contributing towards our knowledge on the freshwater invertebrate fauna (Rotifera & Crustacea) of Botswana and southern Africa. Results from both projects have been presented at national and international conferences and workshops (West & Van As 2008; West *et al.* 2008; 2011a; 2011b; 2011c; 2012a; 2012b; 2013; 2014) and thus far has led to a number of scientific publications (West *et al.* 2015; in press).

Following this brief introduction (**Chapter 1**), a comprehensive description is provided of the study area referring to its geographical position and climatic conditions, as well as the physical shape, functioning, flooding patterns and geological formation of the waterways relevant to the study (**Chapter 2**). **Chapter 3** provides a literature review and background information (which encompasses the classification, systematics, morphology and reproduction) on the various groups of organisms included in the study. In **Chapter 4**, the materials and methods used in the present study are described. **Chapters 5**, **6** and **7** include lists of the Rotifera, Cladocera and Copepoda taxa, respectively, collected from the Okavango Delta and its associated basins. These chapters also include the distribution ranges of the identified taxa within the study area. In **Chapter 7**, distribution maps and photomicrographs for members of the family Cyclopidae were omitted, as there is a shortage of recent literature for southern African freshwater cyclopoids and identification requires further attention. However, a species list is provided of the cyclopoids collected in the study area in order to present new records. The Nata River is dealt with as a separate unit in the form of two scientific papers in **Chapter 8**. The first has been prepared for submission to the *African Journal of Aquatic Science*, while the second has been accepted for publication in *Acta Parasitologica*. The thesis is concluded with a general discussion and concluding remarks (**Chapter 9**), followed by the abstracts, acknowledgements and appendix. **Appendix 1** contains a table which provides the physical water quality parameters recorded at all study sites.

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Chapter 2

THE FLOODING OF A DESERT

Africa covers more or less 30 million km², the majority of which ranges from equatorial rain forests to arid savannas, but one third of the continent consists of desert areas (Welcomme 2003). South of the equator, it is a land of climatic contrasts with the northern parts being wet and tropical, the south temperate, the east mesic and most of the west hyper-arid. Dry conditions dominate much of southern Africa, as almost the entire region is without significant rainfall for at least several months per annum; rainfall in the south and west is episodic and very unpredictable; and evaporation surpasses rainfall throughout most of the region. In short, it is a subcontinent which suffers from a serious water deficit and severe, periodic droughts (Day 2003).

Southern Africa has largely escaped major periods of glaciation since the Permian (290 to 248 million years ago) and consists of a central plateau which is elevated, relatively flat and unbroken. It is due to this that deep valleys and large lakes are not common, with the exception of the African Rift Valley in the north-east and the coastal plains (Day 2003). The entire continent, however, is drained by a series of major rivers (Fig. 2.1) which have been significant in the demography of Africa, determining centres of occupation, transport and cultural exchange (Welcomme 2003). Furthermore, together with their fertile floodplains, these rivers provide fish, reeds, wood, medicines, grazing for livestock and other resources to human populations, the majority of whom live in poverty.

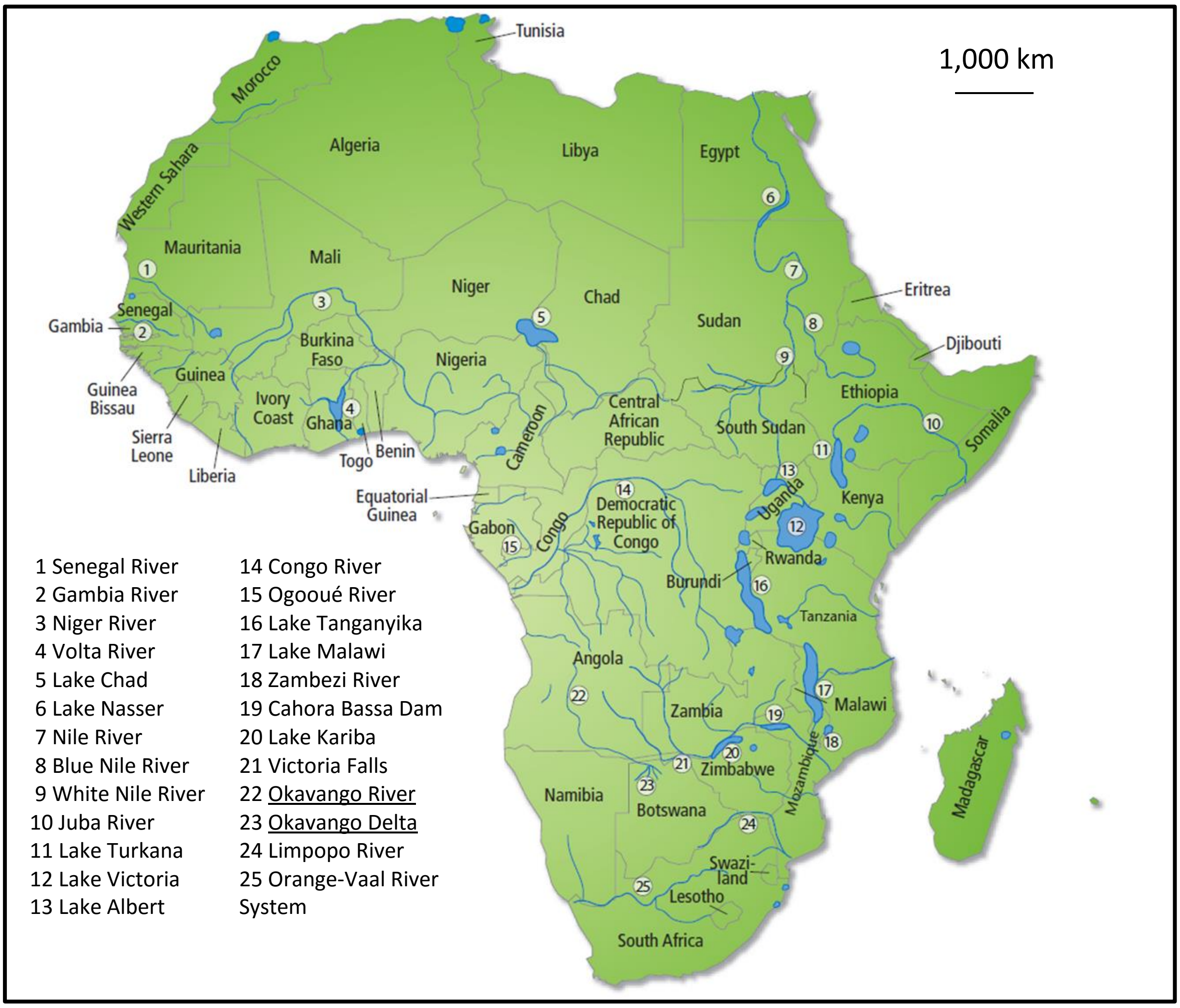

Figure 2.1: Africa is drained by a series of major river systems, most of which are shared by more than one country. These river systems provide vital resources to human populations of the continent (adapted from Van As *et al.* 2012).

Almost all the major rivers of Africa flow through dry regions for at least part of their course, with the exception of some coastal rivers in West Africa and the Congo-Zaire System (Welcomme 2003). Africa has three major deserts (the Sahara, Namib and Kalahari), amongst others, which cover more than a third of the continent. This study was conducted in the southernmost, largest and probably most captivating of the African arid environments - the Kalahari Desert.

THE KALAHARI DESERT

The ‘Kalahari’, which has been described as a desert, thirstland and sandveld, represents an ill-defined area in the interior of southern Africa (Thomas & Shaw 1991). The Mega Kalahari or Kalahari Basin (Fig. 2.2) encompasses the Kalahari Desert which covers an area of about 2.5 million km^2, making it the largest continuous sea of sand on earth, and stretches from southern Angola, across most of Botswana, into eastern Namibia and all the way south to the Orange River in South Africa (Fig. 2.2) (Thomas & Shaw 1991; Ross 2003; Van As *et al.* 2012).

The Kalahari comprises a striking range of landforms, from vegetated dunes (Fig. 2.3A) and mountainous outcrops with caves (Fig. 2.3B), to pans (shallow, natural depressions which contain clay and silt and hold water after rain), ancient lakes and a network of fossil valleys which are an indication of long-term climatic change in the region. Kalahari landscape records of travellers such as David Livingstone and James Chapman suggest that seasonal water sources, namely river valleys and pans, provided vital centres along the routes across this thirstland (Nash 1996).

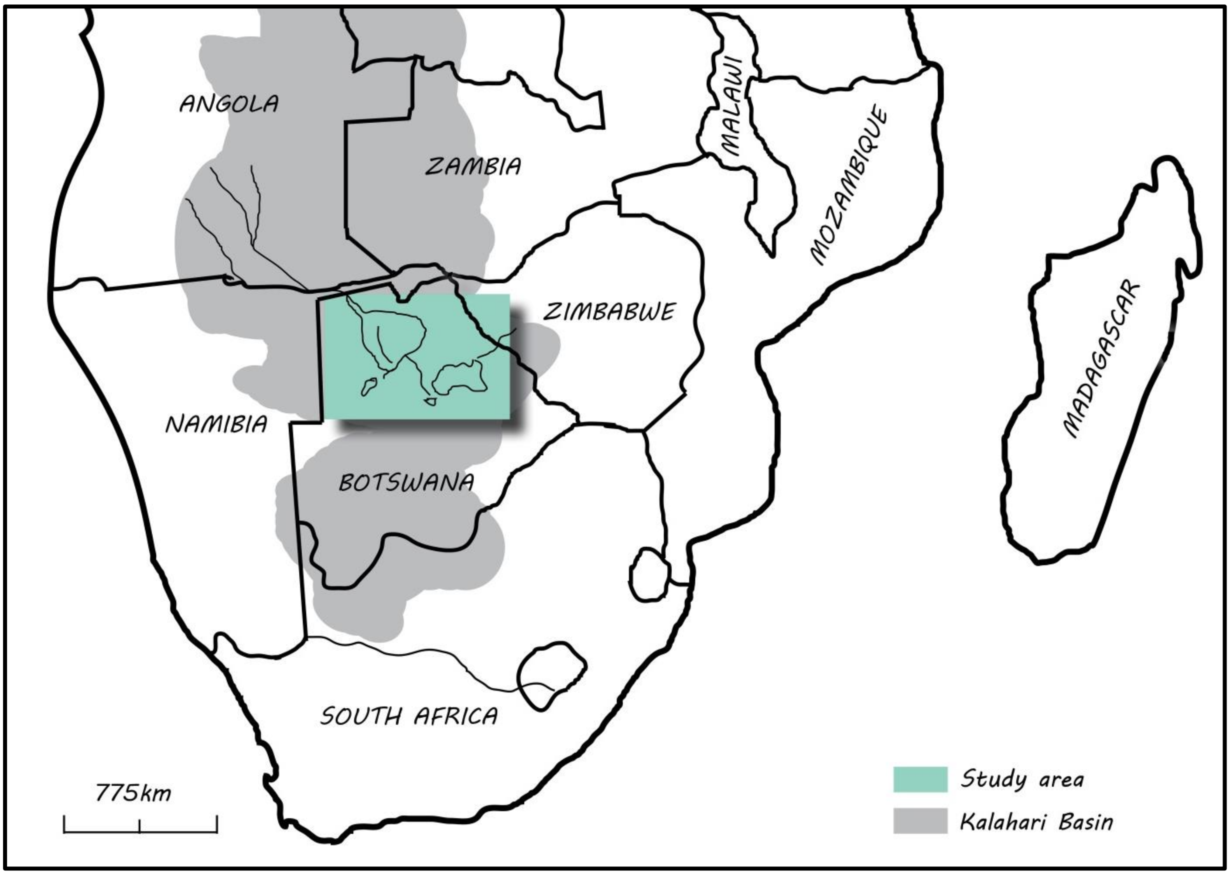

Figure 2.2: The Kalahari Basin which stretches for hundreds of kilometres in the heart of southern Africa and the position of the study area within the Kalahari Desert.

GEOLOGICAL HISTORY

The Kalahari Desert began to form during the division of Gondwanaland in the Mesozoic (248 to 65 million years ago) when tectonic activity caused rifting in south-eastern Africa and consequently influenced the nature of sedimentation in parts of southern Africa. Later, during the final division of Gondwanaland, from the mid-Jurassic (206 to 142 million years ago) to early Cretaceous (142 to 65 million years ago), earth movements were gentler and allowed for downwarping in the coastal zone and interior of the continent. This caused the development of basins in the interior of southern Africa and it is in the southernmost of these that Kalahari sediments eventually accumulated (Thomas & Shaw 1991).

SOIL AND VEGETATION

The Kalahari Sands, which mantle the surface of this characteristically flat landscape (Fig. 2.3A), reach thicknesses of more than 400 m in some places. Sand is perhaps one of nature’s harshest habitats as it drains water like a sieve and over millennia nutrients are lost with the water seepage. Therefore, the Kalahari Sands can be described as weakly developed and the floral communities tend to be resilient, adaptive and low in diversity. Given the soil characteristics and mean moisture deficit, it is surprising that the Kalahari is relatively well-vegetated (Thomas & Shaw 1991; Ross 2003). Annual and perennial grasses such as *Aristida*, *Stipagrostis* and *Eragrostis* dominate the vegetation and shrubs and trees occur in apt habitats. On the banks of ephemeral rivers, the riparian habitat is dominated by trees such as *Vachellia erioloba* and *Faidherbia albida* (Figs. 2.3C & 2.3D) (Van As *et al*. 2012).

CLIMATE

The semi-arid Kalahari Desert experiences hot summers and winters with warm days and cold nights, but the variations in precipitation contribute more to seasonal contrasts in climate than temperatures do. It is, therefore, more appropriate to refer to wet and dry seasons, than to summer and winter (Thomas & Shaw 1991). Contrasts between dry and wet seasons and cycles of drought and abundant rainfall are substantial (Van As *et al.* 2012).

The entire desert is a summer rainfall zone, with 80% of the annual rainfall occurring between October and April. The length and onset of the wet season varies spatially and in Botswana the rains most often do not begin until late November. Rain mostly occurs in the late afternoons and early evenings in the form of high-intensity thunderstorms (Figs. 2.3E & 2.3F), but not every rainfall event is significant as volumes are less than 10 mm for more or less 50% of these showers (Thomas & Shaw 1991). Precipitation increases from south to north and from west to east, with the driest south-western areas receiving as little as 150 mm of rainfall per annum, the northern areas between 500 and 800 mm (Van As *et al*. 2012) and the north-eastern corners about 650 mm (Thomas & Shaw 1991).

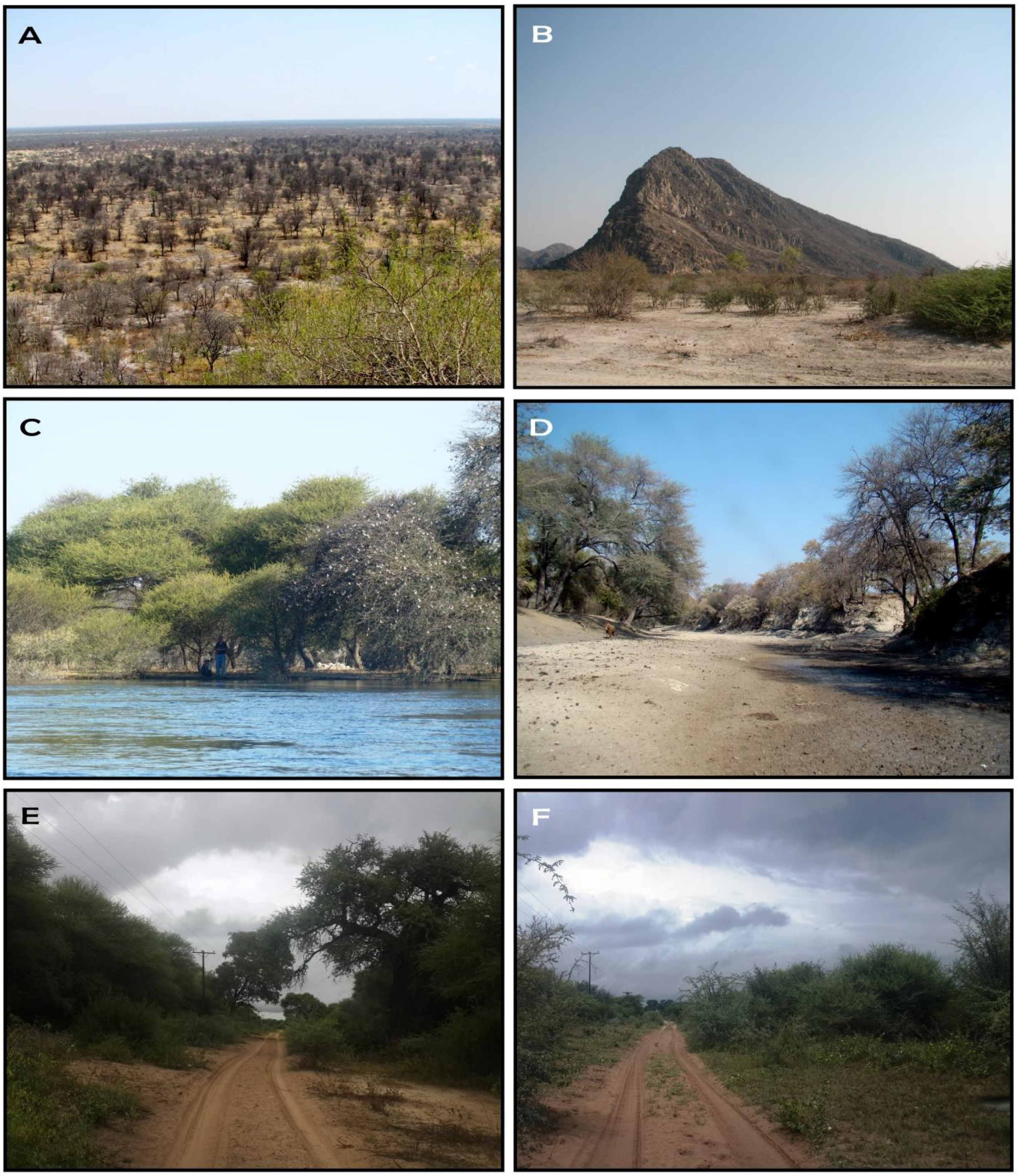

Figure 2.3: The Kalahari environment in northern Botswana. **A**: The flat landscape and vegetated dunes. **B**: Mountainous outcrops with caves at Tsodilo Hills (Courtesy of Hanli Groenewald). **C** & **D**: Typical riparian habitat of ephemeral rivers. **C**: The Lake River entering Lake Ngami. **D**: The Nata River. **E** & **F**: Heavy clouds building before a late afternoon thunderstorm in the vicinity of the Okavango Panhandle.

The desert conditions of the Kalahari are not only caused by low rainfall, but also high average annual evaporation rates. In most parts of the Kalahari Desert evaporation rates exceed 2,000 mm per annum, while values exceed 4,000 mm in the south-western areas, where the potential exists to evaporate between four and 10 times the annual rainfall. This results in a moisture deficit during all except the wettest months (Thomas & Shaw 1991).

The Kalahari Desert, therefore, has a lack of permanent, and even seasonal, water bodies. It does, however, contain beds of ancient lakes which cover an area the size of Belgium and the Netherlands combined (Thomas & Shaw 1991) and, surprisingly, also southern Africa’s largest wetland and the world’s most extensive alluvial fan or inland delta – the Okavango Delta.

THE OKAVANGO RIVER AND DELTA, AND ASSOCIATED BASINS

Worldwide, rivers flow to finally meet the ocean, washing their freshwater into it. In southern Africa, however, lies a river that does not spill its water into the ocean, but that has it spread across the dry, nutrient-poor sands of the Kalahari Desert instead. This is one of Africa’s major and most pristine rivers, the Okavango (Figs. 2.1 & 2.4).

It is a relatively underdeveloped hydrological system (Kniveton & Todd 2006) and most definitely one of the least developed river basins in Africa (Andersson *et al.* 2006). The Okavango Basin is occupied by 14 major ethnic groups with different cultures (Kgathi *et al*. 2006) and supports livelihoods through water supply, irrigation, horticulture and tourism, amongst others (Kniveton & Todd 2006). It is the fourth largest international basin in southern Africa (Hitchcock 2003) and stretches across an area of 192,500 km² (Mendelsohn & El Obeid 2004; Van As *et al.* 2012), within the borders of Angola, Namibia and Botswana where it is of critical importance to the well-being of its people and animals.

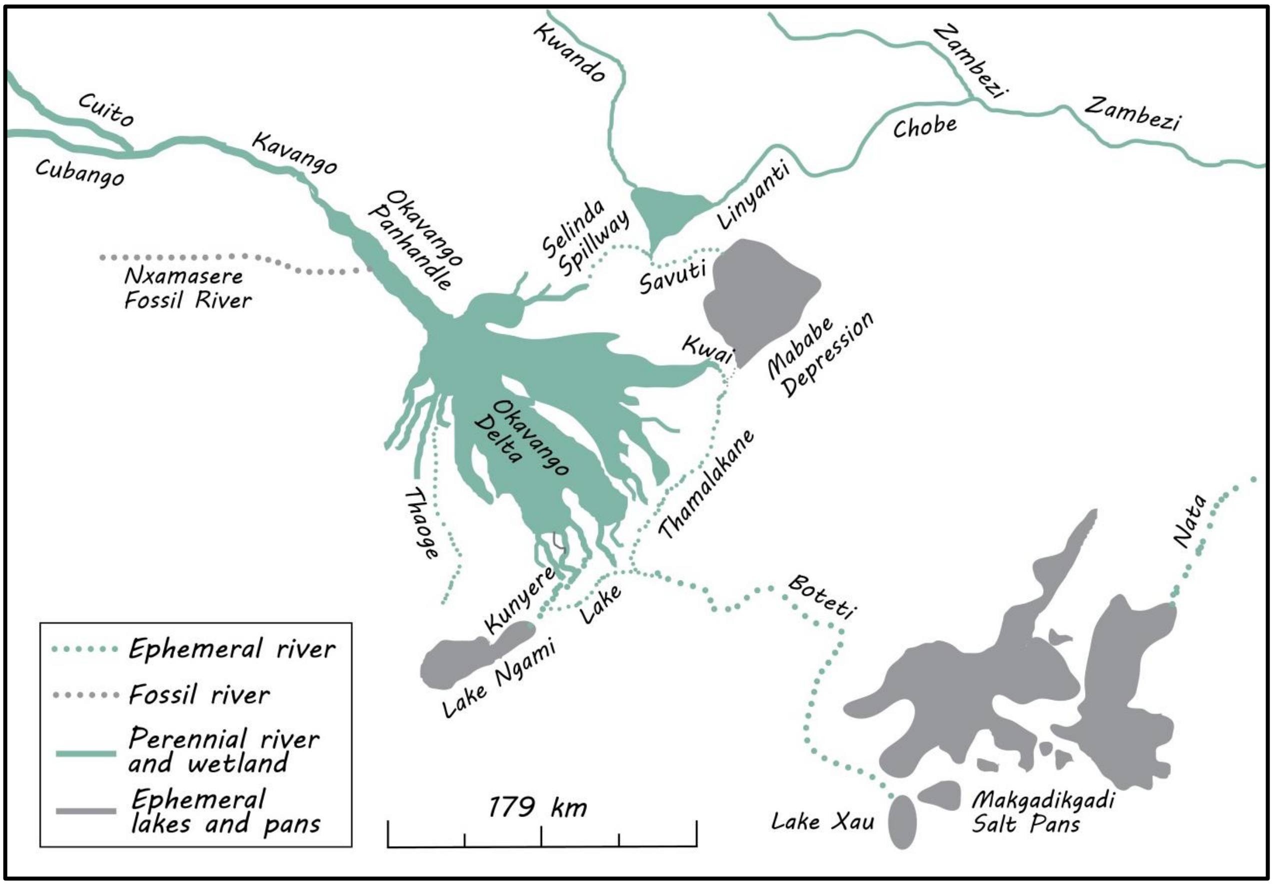

Figure 2.4: The Okavango River Basin is shared by three countries. The entire catchment is in southern Angola where it flows as many tributaries. Thereafter, it flows as a single river through Namibia before entering Botswana and spreading across the Kalahari Sand to form the world's largest alluvial fan. The Okavango Delta is associated with a number of ephemeral water bodies within northern Botswana, including Lake Ngami, the Mababe Depression, Lake Xau and the Makgadikgadi Pans.

THE CATCHMENT (CUBANGO AND CUITO RIVERS)

The Portuguese describe south-eastern Angola as "the place at the end of the earth" (*as terras do fim do Mundo*). It is a remote, wild area which has suffered the effects of war (Fig. 2.5A) and corruption and from which the Okavango water springs (Fig. 2.5B) (Mendelsohn & El Obeid 2004). In the Angolan part of the Okavango System rainfall is highest and water is plentiful and relatively unexploited. Here, in the southern highlands of this remote country, the river starts as many tributaries which flow approximately 1,000 km through valleys (Fig. 2.5C) that vary in width from 0.25

to 1.5 km (Kgathi *et al*. 2006) and eventually merge to become two large rivers, the Cubango (Fig. 2.5A) and Cuito (Fig. 2.5D). These two rivers have a combined catchment of approximately 112,000 km^2 (Mendelsohn & El Obeid 2004; Kgathi *et al.* 2006). The Cubango River eventually forms the border between Namibia and Angola (Fig. 2.5E) for a few hundred (more or less 350) kilometres before it is joined along this course by the Cuito (Fig. 2.5F).

THE KAVANGO RIVER

As a single river making its way towards Botswana, the Okavango flows over a rocky area for about 60 km, through the Caprivi Strip of Namibia, where it is known as the Kavango River (Fig. 2.6A). This stretch of the river is marked by a quartzite ridge (Thomas & Shaw 1991) which is topped to form a series of rapids known as the Popa Falls (Fig. 2.6B). In contrast to Angola, Namibia is a water-scarce country and therefore this part of the river is densely populated. Mendelsohn & El Obeid (2004) state that the river merely flows through Namibia and that all the water that enters Botswana originates in Angola, resulting in maximum flow being between the Cubango / Cuito confluence (Fig. 2.5F) and Mohembo at the border between Namibia and Botswana (Fig. 2.7).

FLOODED DESERT: THE OKAVANGO PANHANDLE AND DELTA

Shortly before entering Botswana, the Okavango River, as it is now called, begins to disperse and form a delta or an alluvial fan (Figs. 2.4 & 2.7). On entering Botswana at Mohembo the river is approximately 200 m wide and 4 m deep (Kniveton & Todd 2006) and is confined within a broad floodplain or depression which is known as the Okavango Panhandle. The river meanders widely for about 300 km, or 150 km as the crow flies, across this floodplain of papyrus swamps (Figs. 2.6C, 2.6D, 2.6E & 2.7). The panhandle is confined between two parallel faults (Fig. 2.7), 15 to 20 km apart, between which the water floods the land causing the main channel to be flanked by papyrus swamps that are scattered with oxbow lakes (Fig. 2.6F), lagoons and side channels (Fig. 2.8A).

Figure 2.5: **A**: Bullet holes in a bridge over the Cubango River in Angola paint a picture of war. **B**: The Okavango water springs from the highlands of Angola. **C**: Angolan valleys through which the Okavango's tributaries flow. **D**: Cuito River, Angola. **E**: The Cubango River forms the border between Angola and Namibia for about 350 km. **F:** Along the Cubango River's course as border between Angola and Namibia it is joined by the Cuito River after which it is known as the Kavango River.

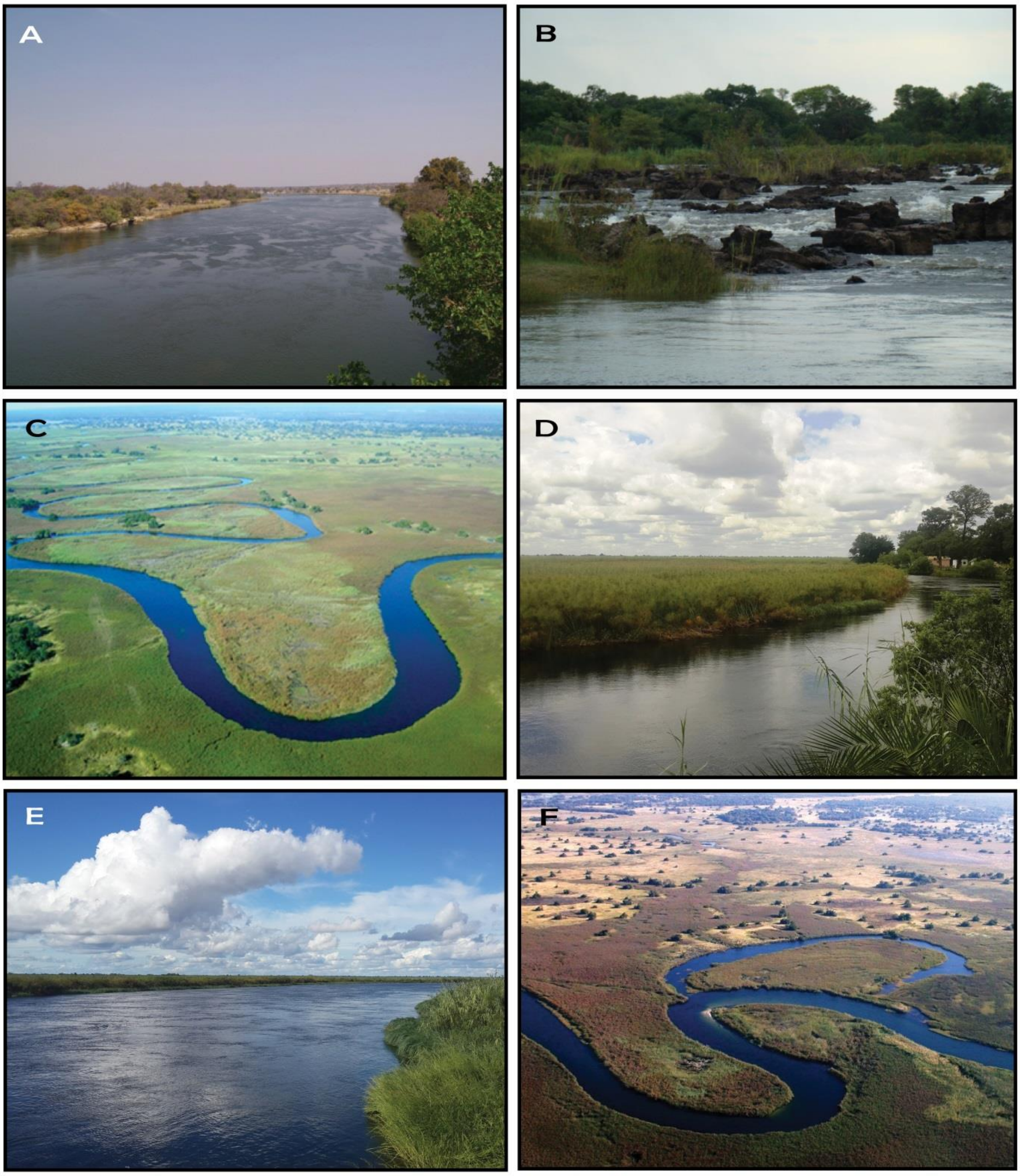

Figure 2.6: **A**: The Kavango River at Divundu, Namibia. **B**: The Kavango River flows over a rocky area in the Caprivi Strip, Namibia, called Popa Falls. **C**: The Okavango River meanders widely within the floodplains of the panhandle in Botswana. **D**: Papyrus swamps of the Okavango Panhandle, Botswana, at the village of Sepopa. **E**: The Okavango River in flood at Samochima in the panhandle. **F**: The papyrus swamps in the panhandle are scattered with oxbow lakes.

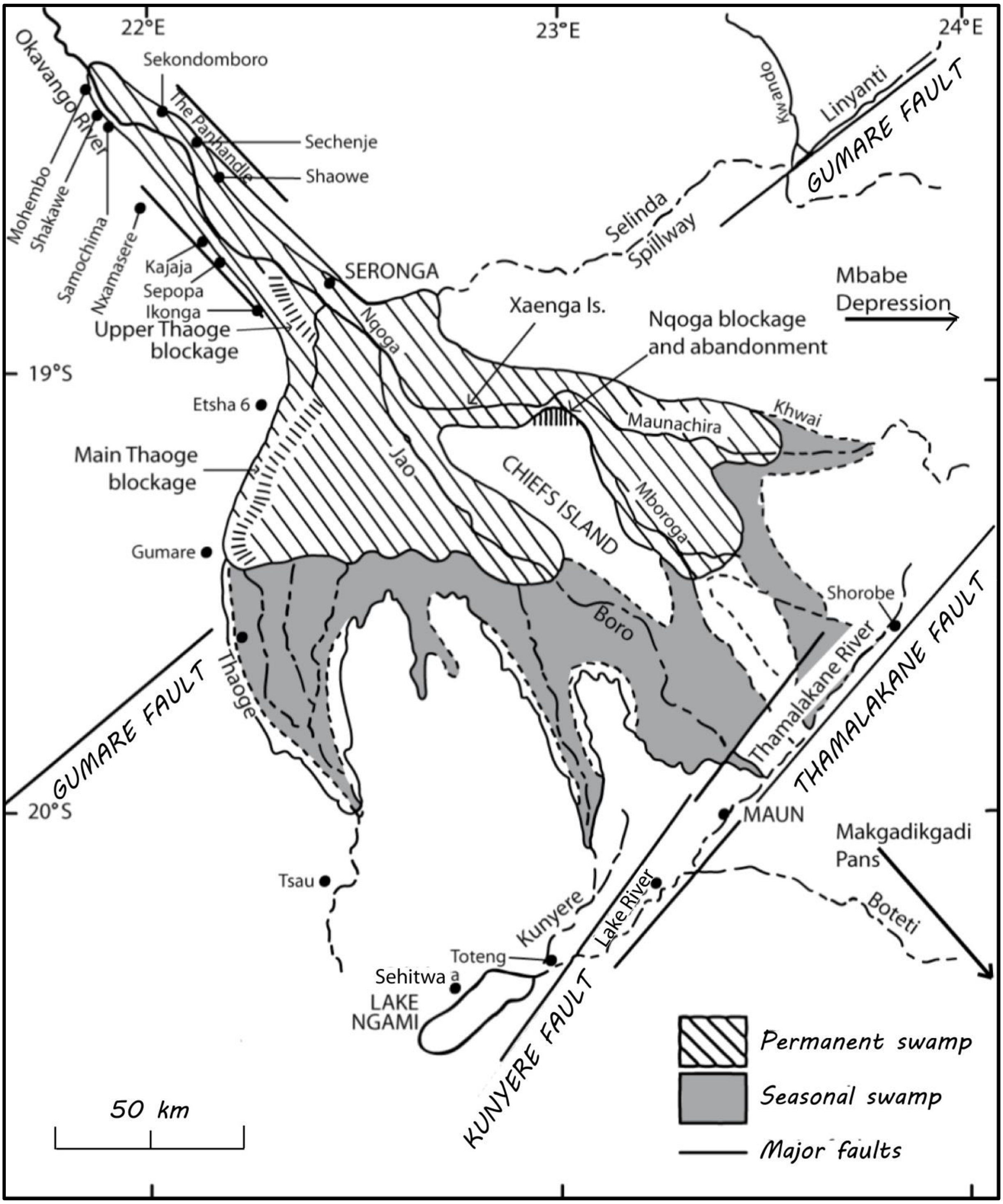

Figure 2.7: Main features of the Okavango Delta, including the faults controlling its shape, Okavango River within the panhandle, major channels in the delta fan, outflows towards other water bodies closely associated with the delta, Lake Ngami and towns and villages along the panhandle and elsewhere in and around the delta (redrawn from Thomas & Shaw 1991).

An estimated 40% of the total volume of water leaks into the surrounding swamps while, at the southern end of the panhandle, the remaining 60% flows over the east-west oriented Gumare Fault (Fig. 2.7) and spreads out into a number of distributary channels, creating a mosaic of land and water known as the Okavango Delta Fan (Figs. 2.8B & 2.8C) (Mendelsohn & El Obeid 2004).

The most easterly channel, the Nqoga, carries 63% of the water entering the delta fan which is later further dispersed along the Maunachira, Mboroga and Santantidibe distributary channels. The central channel, the Jao, carries 21% and the most westerly channel, the Thaoge, 16% of the water entering the delta fan (Fig. 2.7). Between the main channels are floodplains, swamps and tongues of sand and the margins around the entire delta are hard to define due to the varied flooding from year to year and the outlying areas only being inundated during years of exceptional floods (Mendelsohn & El Obeid 2004).

The permanent swamps form the core (upper north and central areas) of the alluvial fan and extend over an area of between 2,000 and 3,000 km². Unlike the panhandle, where water fluctuates up to two meters during the year, levels are relatively constant in the permanent swamp. Here, water mainly flows along channels from which it slowly leaks into large areas of papyrus, reeds and sedges. The permanent swamps are also dotted with many ancient oxbow lagoons. The southern, western and eastern areas of the delta fan are covered by seasonal swamps which are flooded by water from the permanent swamps. It flows as sheet flooding, less than half a metre deep and spreads slowly across the landscape (Figs. 2.8B & 2.8C). Higher ground forms temporary islands and plant communities are more diverse in these seasonal swamps as different species favour patches with a different duration and depth of flooding. The vastness of the seasonal swamps naturally depends largely on the inflow from the Angolan Highlands and the extent of local rainfall and, therefore, varies greatly between 4,000 and 8,000 km² from year to year (Mendelsohn & El Obeid 2004).

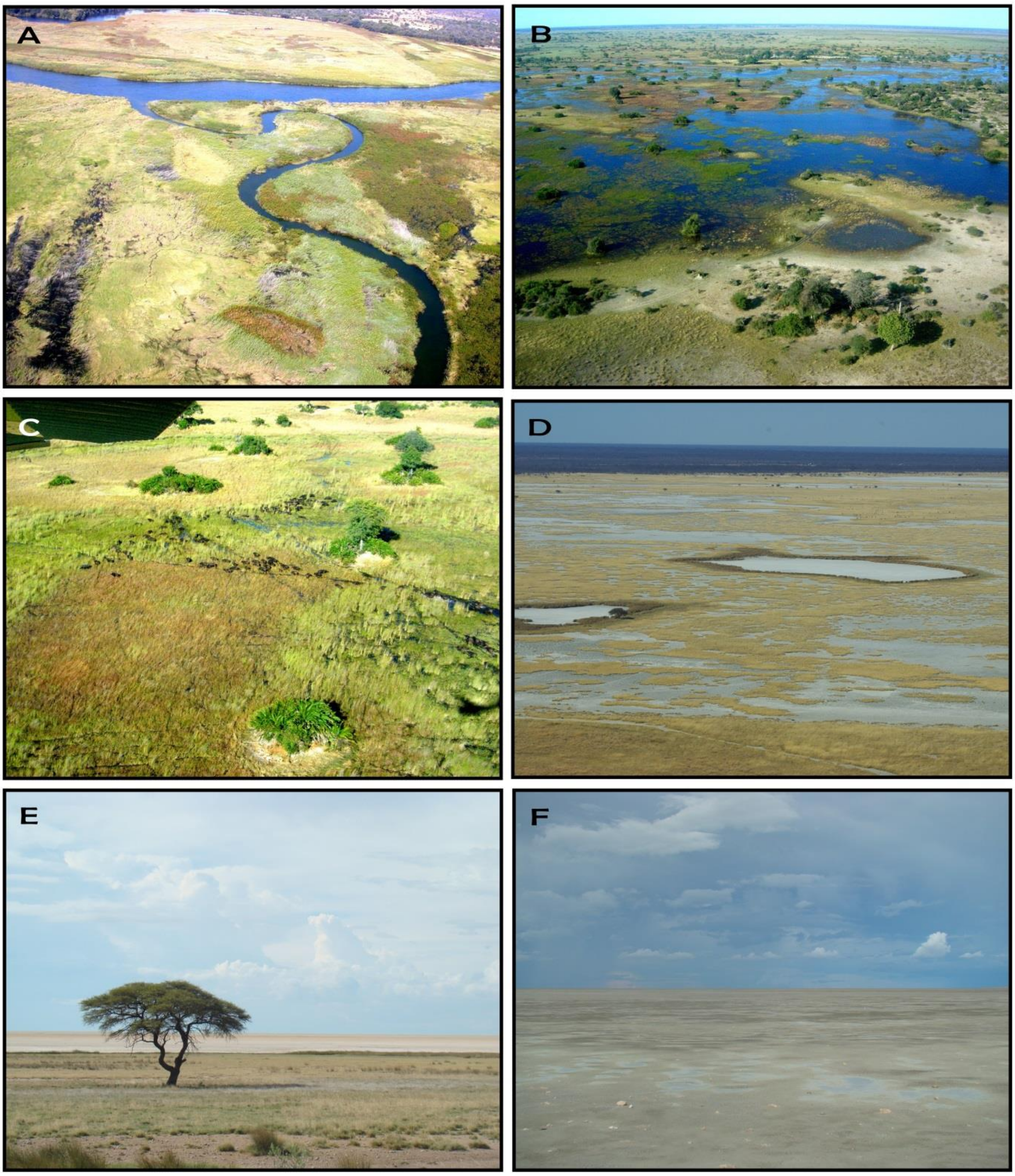

Figure 2.8: **A**: Mainstream and side channel in the Okavango Panhandle. **B** & **C**: Sheet flooding less than half a metre deep spreads slowly across the Okavango Delta Fan. **D**: In arid environments salt becomes concentrated in most wetlands and forms crusts, such as in the Makgadikgadi Pans, Botswana. **E** & **F**: Landscape of the Etosha Pans, Namibia.

FAULTS IN THE LANDSCAPE AND THE SHAPING OF AN OASIS

The current shape of the delta is maintained by a series of parallel faults (Fig. 2.7) which form the southern extension of the East African Rift Valley. This feature extends from the Red Sea to the Okavango Delta in Botswana (Van As *et al.* 2012). It is now most prominent in East Africa and Malawi, while deep valleys have never formed in Botswana and Namibia, as the arm extending into these countries has most likely not been activated adequately. As previously mentioned, two parallel faults control the orientation of the river in the panhandle and are at right angles to the main structural trend (Thomas & Shaw 1991). The Gumare Fault (Fig. 2.7) directs the river's exit into the delta fan from the panhandle as it breaks the land causing the water of the Okavango to spread across the Kalahari Sand. At the distal margin of the delta its water is halted once more by two northeast-southwest trending faults, the Kunyere and Thamalakane (Fig. 2.7), which redirect the water in the direction of other water bodies in the Kalahari closely associated with the delta (Figs. 2.4 & 2.7). Kgathi *et al.* (2006) stated that the faults are seismically active and some appeared to be extending at a rate of approximately 2 mm/year.

The Okavango River, however, has undergone a series of changes during its geological history. It is believed that southern Africa was elevated at the time Gondwana was breaking up. A marginal escarpment was formed between the elevated interior and the newly formed coastal plains by rifting and the formation of seaways around the subcontinent. This escarpment was raised slightly relative to the interior. The climate was comparatively warm and humid during the Cretaceous (142 – 65 million years ago) and vast tropical and sub-tropical forests were present in southern Africa. A drainage network involving three major river systems, the Limpopo, Karoo and Kalahari Rivers, was formed in the interior of the subcontinent (Fig. 2.9) (McCarthy & Rubidge 2005). The most extensive of the three major rivers, known as the Limpopo River, drained the vast northern regions of southern Africa and encompassed the Okavango, Chobe, Kwando, Upper Zambezi and Limpopo Rivers (Thomas & Shaw 1991; Ross 2003; McCarthy & Rubidge 2005; Kgathi *et al*. 2006). Sediment eroded from the Limpopo River System's immense catchment and was deposited along the Mozambique coast where it formed a massive delta. The Lower Zambezi stood on its own on the east coast of southern Africa, separate from the three major rivers. The second and third major rivers, the Karoo and Kalahari Rivers, both flowed to the west and drained the eastern highlands and the western interior, respectively. The escarpment, on the other hand, was drained by many short rivers (Fig. 2.9) (McCarthy & Rubidge 2005).

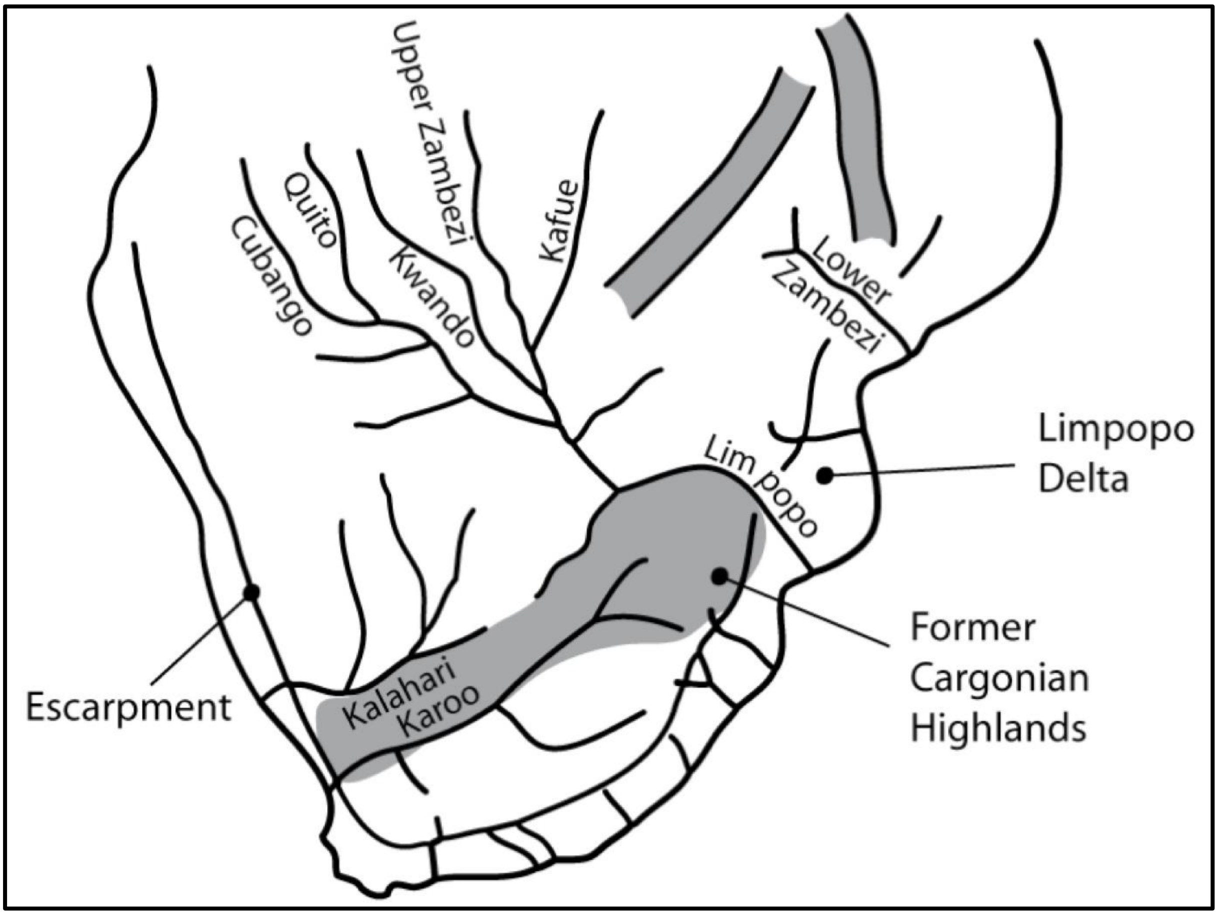

Figure 2.9: Southern Africa was elevated at the time Gondwana was breaking up, resulting in a marginal escarpment being formed between the interior and the coastal plains, as well as a drainage system consisting of three major river basins, the Limpopo, Kalahari and Karoo Rivers (redrawn from McCarthy & Rubidge 2005).

Gentle arches (axes) began to form in the interior of Africa about 60 million years ago and two of these, the Transvaal-Griqualand Axis and the Kalahari-Zimbabwe Axis, resulted in the formation of the Kalahari Basin. Furthermore, the former rift caused the Karoo River to capture the Kalahari River and form the Orange River System. The Kalahari-Zimbabwe Axis, on the other hand, cut the headwaters of the Limpopo River off and thereby obstructed its flow and caused the damming back of this major river. It was as a result of this that a complex and vast series of swamps and lakes began to form in the interior of southern Africa. The largest of these was Lake Paleo-Makgadikgadi which was similar to the modern Lake Victoria and preceded the present day Makgadikgadi Pans (Fig. 2.10) (Ross 2003; McCarthy & Rubidge 2005).

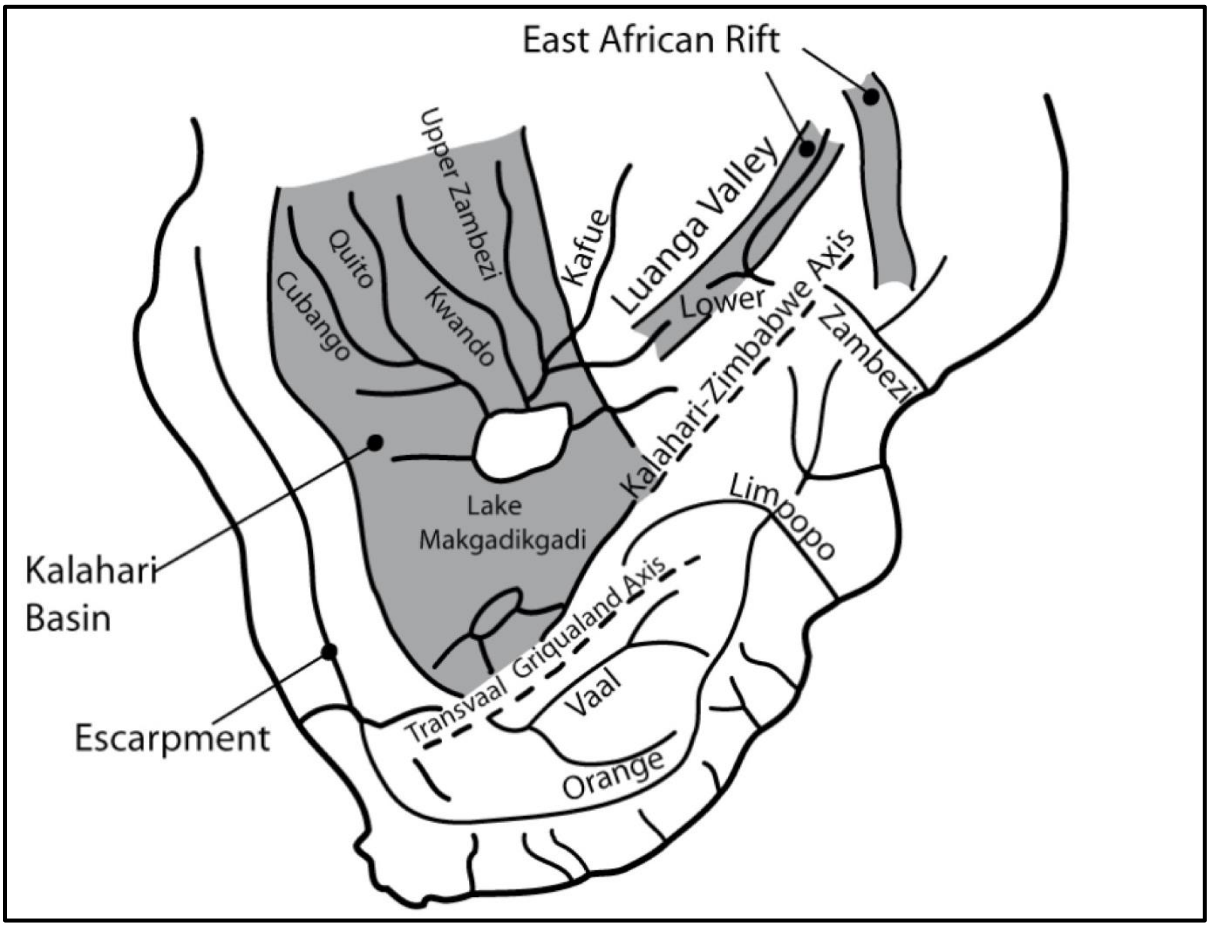

Figure 2.10: The formation of the Transvaal-Griqualand Axis and the Kalahari-Zimbabwe Axis about 60 million years ago resulted in the establishment of the Kalahari Basin, the Orange River and Lake Makgadikgadi (redrawn from McCarthy & Rubidge 2005).

Thomas and Shaw (1991) stated that there is sufficient data available to indicate that periods of extensive lakes were interspersed with periods of Aeolian activity and that there were two major lake stages. The higher of these two stages was Lake Palaeo-Makgadikgadi, at the 940 to 945 m level, which encompassed the lower Okavango Delta, Lake Ngami, the Makgadikgadi Pans and the Mababe Depression. Estimates of its size vary from 60,000 to 80,000 km² and it represents the fossil lake at its utmost extent. The second stage was termed Lake Thamalakane and most likely had an area of more or less 7,000 km² in the region of the delta. At times it would most likely have overflowed to the Makgadikgadi Basin, in which case it would have supplied either the 920 m or the 912 m level. Below this level the lake would have split into separate basins with separate responses to climate and hydrology.

About 20 million years ago central southern Africa began to rise. This continual upliftment has resulted in a topographic abnormality of global significance in that areas of similar geology and geological history lie at 300 to 400 m above sea level, while large areas of southern Africa have elevations of more than 1,000 m above sea level. This topographic abnormality has formed far from any tectonic plate boundaries and is therefore difficult to explain using plate tectonics. Earth scientists have been using sensitive seismometers which record seismic waves from distant earthquakes to investigate this feature and have dubbed it the African Super Swell (McCarthy & Rubidge 2005).

It turns out that there is an enormous 'blob of hot material', nearly 2,000 km in diameter, in the mantle beneath southern Africa. It appears to be rising to the surface much like a bubble in thick syrup rises. The earth's surface is therefore being pushed up, forming the Super Swell. The 'blob' has a tail like a giant tadpole, which is causing rifting and the formation of the East African Rift Valley in the region in which it lies (McCarthy & Rubidge 2005).

There were two main periods of uplift in southern Africa during which the eastern portion rose more than the west. At the time of the first (20 million years ago), the east rose by more or less 250 m, while the west rose by about 150 m. Approximately 14 million years ago the upwelling of cold water began on the west coast, causing extremely arid conditions to develop in the area and lakes in the Kalahari Basin began to dry. Furthermore, the drying of these lakes was intensified by the Zambezi River which progressively captured their major tributaries and finally the lake and river deposits in the Kalahari was replaced by desert sand (Fig. 2.11). This was followed by the second uplift of southern Africa which took place approximately five million years ago and caused the east to rise by 900 m and the west by a mere 100 m. Due to the eastern escarpment being comparably higher, moist air from the Indian Ocean lost a lot of its water as it rose against the escarpment, causing a rainfall reduction in the interior of southern Africa and increasing the difference between rainfall in the east and west even more (McCarthy & Rubidge 2005).

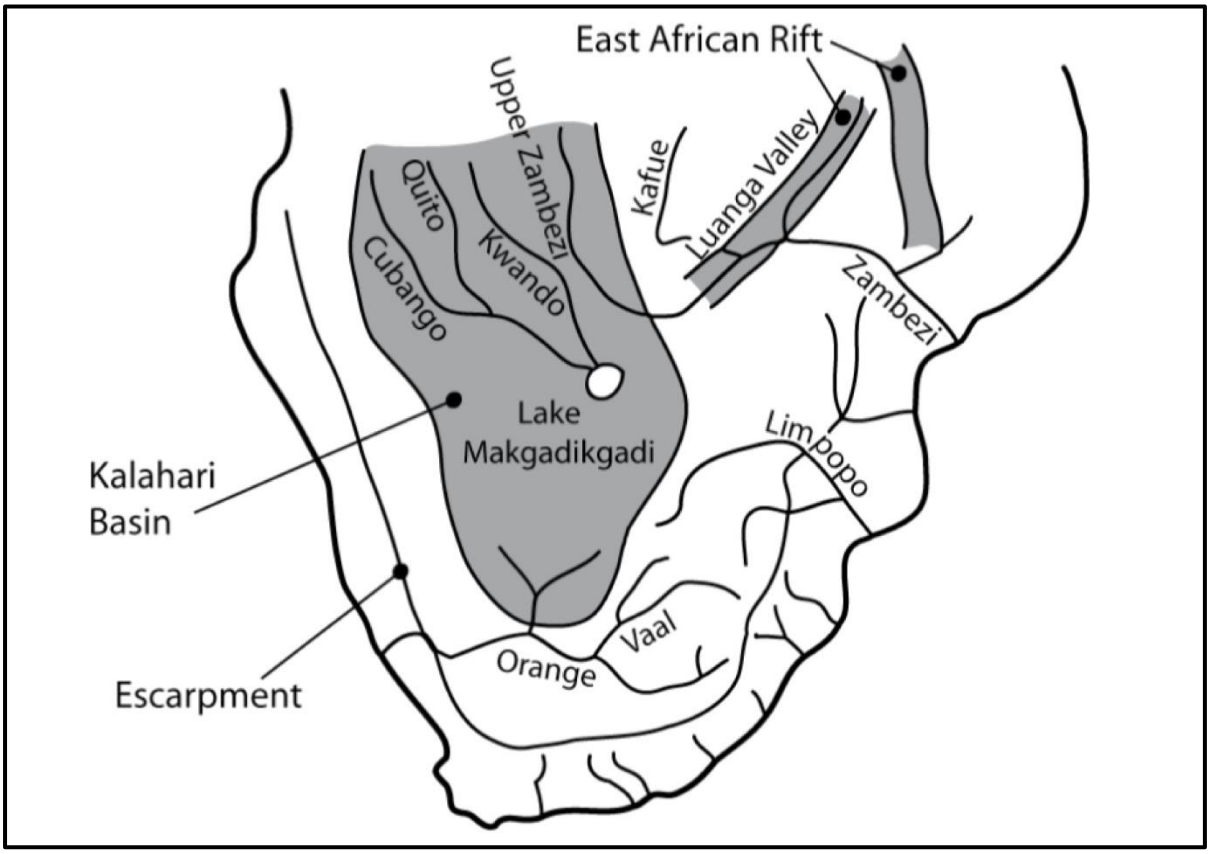

Figure 2.11: Approximately 14 million years ago lakes in the Kalahari Basin began to dry and the Zambezi captured their major tributaries, intensifying the dryness of Lake Makgadikgadi (redrawn from McCarthy & Rubidge 2005).

Rifting in East Africa continues to take place and has been responsible for the faulting which has caused major changes in the waterways of southern Africa. The Kwando River diverged into the Zambezi and the Upper and Lower Zambezi Rivers merged, while the Okavango River simply entered the flatness of the Kalahari (Ross 2003; McCarthy & Rubidge 2005; Kgathi *et al.* 2006; Burrough & Thomas 2008), slowed down, deposited its sediment and formed an alluvial fan or inland delta in northern Botswana (Fig. 2.12). The Okavango Delta's characteristic fan shape was formed by the blocking of channels and water following other courses and continuing to deposit sediments within a fault-controlled basin (Ross 2003). This is the last surviving remnant of the once great Lake Paleo-Makgadikgadi.

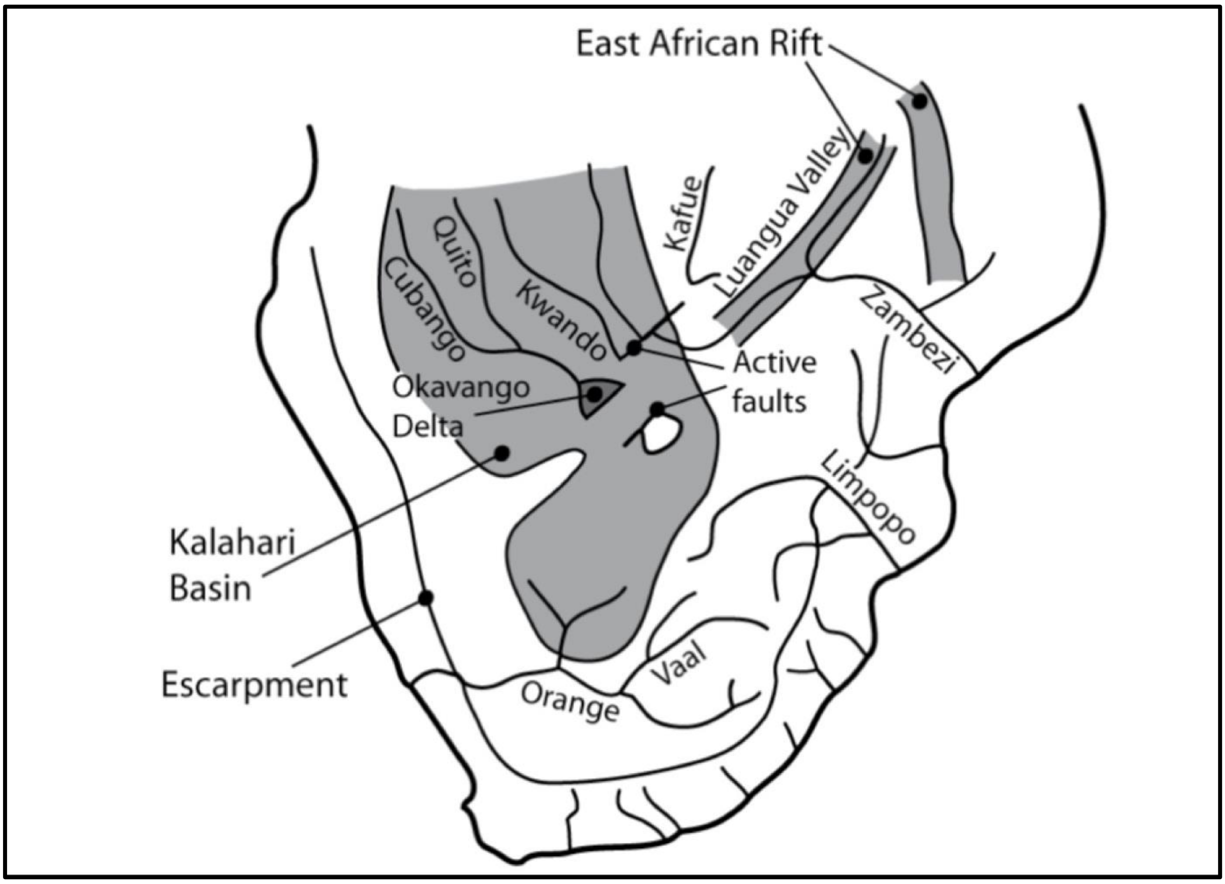

Figure 2.12: Rifting in East Africa and the consequent faulting led to the Kwando River diverting into the Zambezi and the merging of the Upper and Lower Zambezi Rivers, while the Okavango River slowed down and formed an alluvial fan in the Kalahari Desert (redrawn from McCarthy & Rubidge 2005).

CURRENT FUNCTIONING OF THE OKAVANGO

The Okavango as we know it, functions in a unique manner. In hot and arid areas, salt becomes concentrated in most wetlands and forms crusts. Sodium concentrations can reach levels as high as 500 mg/L in areas with low rainfall (WRC 1998). The Makgadikgadi Pans (Figs. 2.4 & 2.8D), south-east of the delta, and the Etosha Pans (Figs. 2.8E & 2.8F) in Namibia are good examples of this (Mendelsohn & El Obeid 2004).

The alluvial fan has been formed by the water, nutrients and sediments that flow down the Okavango River from Angola (Mendelsohn & El Obeid 2004) and although many of the different compounds carried down the Okavango are salts, its water is exceptionally fresh. In a study on the surface water quality of the entire Okavango Panhandle, from Popa Falls in Namibia to Guma Lagoon in the north-western tip of the delta fan, West *et al*. (2015) found that all nutrient concentrations were extremely low and did not exceed the ideal water quality ranges for a number of uses as set out in the Water Quality Guidelines of South Africa (DWAF 1996a-e). In fact, concentrations of a number of nutrients, such as bromide, nitrogen from nitrite and phosphorus were below detection limit. The electrical conductivity in the panhandle, including drying floodplains with high evaporation rates, never exceeded 28.3 mS/m between December 2006 and January 2009 (West *et al.* 2015).

The Okavango owes its fresh water to a number of factors. The most important of these is the annual pulse flooding of the system.

RAINFALL

The area in which the Okavango lies experiences low and erratic rainfall, in the region of 500 mm per year, and high potential evaporation rates which are five to six times that of the rainfall (Garstang *et al.* 1998; Ashton *et al*. 2003; Kgathi *et al.* 2006). Rainfall mainly occurs between November and March, but may be scarce or completely absent in some years. The build-up to rain lasts for months before it eventually comes as a dramatic, long-awaited event (Ross 2003). In Botswana, the value placed on rain is evident. The name of the country's currency is *Pula* which means 'rain', while the word for small change is *Thebe* meaning 'small droplets'.

The delta's water and vegetation creates its own climate and it has more rain than other parts of the Kalahari (Ross 2003). This local rain provides a third of the water in the delta, but it has a minor impact in comparison to a distant rain-born event – the annual flood.

THE RYTHMIC FLOODING OF THE DELTA

At the top of the catchment, average annual rainfall is more or less three times higher than in the delta and falls mainly between October and April (Mendelsohn & El Obeid 2004). This rainfall in the highlands of Angola provides two-thirds of the delta's water (Thomas & Shaw 1991; Mendelsohn & El Obeid 2004), which after travelling down the Cuito, Cubango and Kavango Rivers enters the Okavango Delta, swells its banks and produces a flood tide.

In the land-locked country of Botswana, the Okavango River empties between 9.4 (Mendelsohn & El Obeid 2004) and 10.6 km^3 (Hitchcock 2003) of water and approximately 590 000 tonnes of sediment (McCarthy & Ellery 1998) across the Kalahari Desert each year. This input from the catchment is supplemented by a further 3.2 km^3 of rain water which falls directly on the delta annually (Van As *et al.* 2012) and there are, therefore, two distinct inputs to the regime. A staggering 96% of this inflow from the Angolan highlands and local rainfall is lost to evapotranspiration and another 2.5% seeps away into groundwater aquifers (Mendelsohn & El Obeid 2004; van As *et al.* 2012) so that the long-term average outflow of 1.5% is estimated to only be between 0.189 and 0.207 km^3 (Mendelsohn & El Obeid 2004).

The highest elevations of the Okavango River in the headwaters are over 1,700 m above sea level while it is 940 m above sea level at the lowest reaches of the delta (Mendelsohn & El Obeid 2004). The gradient of the river becomes gentler downstream, slowing its flow. After entering the panhandle at Mohembo in April, the floods move slowly through the delta covering sandbanks, filling lagoons, inundating floodplains and flushing the papyrus swamps with fresh water. In the delta fan the floods often do not exceed a kilometre a day, not only because of the flat landscape, but also because it is slowed by swamp vegetation, seepage into the ground and the uneven landscape which causes upstream depressions to fill up before water can move on. Due to this, the floods take on average four to five months to travel the length of the panhandle and the delta fan and a very small volume of the water that enters the panhandle eventually reaches Maun (Fig. 2.7) in July. To place this in perspective, the Okavango's water takes a month or two to travel the first 1,000 km or so from the headwaters in Angola to Mohembo, where it enters Botswana, and four months to travel down the last 250 km to Maun (Garstang *et al.* 1998; Ross 2003; Mendelsohn & El Obeid 2004). The maximum flooding of the delta from July to August makes this wetland a true oasis, as by this time the Kalahari Desert which it floods has been without any considerable rain for months.

Variable flows

The precise pattern of flooding differs from year to year and the major factor determining the levels of flooding in the delta is the volumes of inflow from Angola. There are, however, other factors which also play a role and include:

- Local rainfall as it contributes on average 25% of the delta's water.
- The extent of flooding during the previous years as this has an effect on soil saturation and the height of the water table.
- Current evaporation rates which are generally highest during the windy, hot months of September and October (Mendelsohn & El Obeid 2004).

The total volume of water that enters the delta therefore varies from year to year and after it has travelled a number of months, being sucked up by sand, drawn up by the sun and utilised by countless people and other organisms (Figs. 2.13A-F) the last remaining water is lost in the shallow floodplains of the lower delta. The journey, however, does not completely end here.

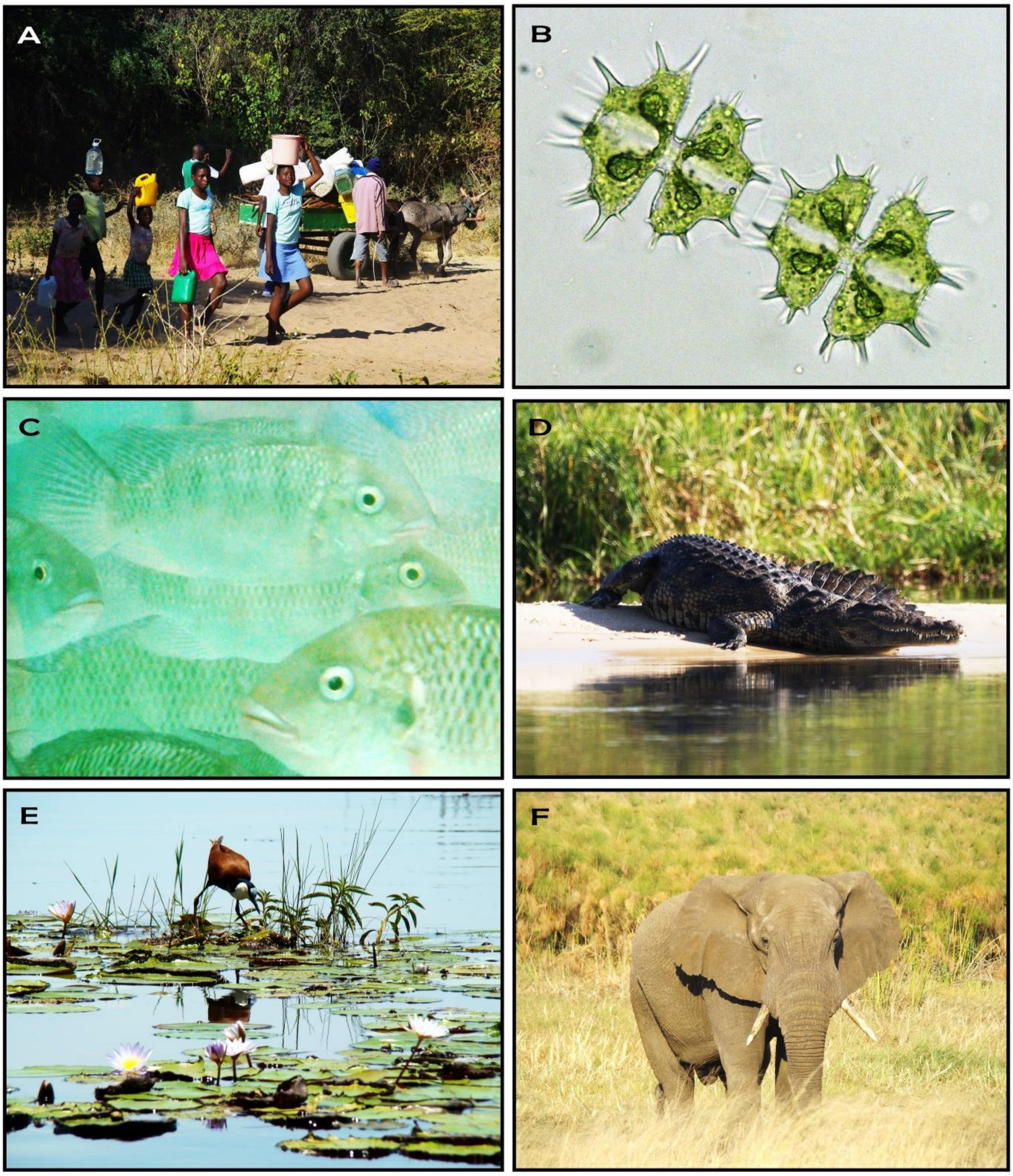

Figure 2.13: **A**: Local inhabitants walk kilometres to fetch water from the Okavango River for all household purposes. **B**: *Xanthidium* (Chlorophyta) collected from the Okavango Panhandle. **C**: Members of the family Cichlidae are good sources of nutrition to the people in the Okavango region. **D**: Nile crocodile (*Crocodilus niloticus* Laurenti, 1768) sunbathing on a sandbank in the upper panhandle. **E**: *Actophilornis africanus* (Gmelin, 1789) (African jacana) hunting for prey on the leaves of water lilies which are common in the stagnant or slow flowing waters of the delta. **F**: *Loxodonta africana* (Blumenbach, 1797) (elephants), amongst others, migrate to the Okavango during the dry season.

OUTFLOW FROM THE OKAVANGO

There have been a number of estimates as to the quantity of water which leaves the Okavango each year. In recent years, low rainfall in Angola has led to low water levels, near drought conditions in the delta and very little to no outflow. More recently (1998 onwards), however, rainfall, water levels and outflow increased, but still remained below long-term average levels (Ashton *et al*. 2003). This changed in 2010 when exceptionally high rainfall in the Angolan Highlands caused the Okavango to swell and overflow to such an extent that a number of major basins within the central Kalahari were inundated as a result. These basins, remnants of the great Lake Paleo-Makgadikgadi, had been bone-dry for a number of decades prior to this major event. They are closely associated with the Okavango and include the Mababe Basin towards the east of the delta, Lake Ngami which lies at the south-western tip of the delta as well as Lake Xau and the Makagadikgadi Pans which are situated deep in the Kalahari Desert more than 200 km from the delta towards the south-east (Fig. 2.4).

It was mentioned earlier that the delta fan comprises a number of distributary channels and these channels all flow in the direction of the Okavango's associated basins and other water bodies. The most easterly distributary, the Selinda Spillway, carries water to the adjacent Linyanti River and hence towards the Zambezi from time to time, while the Maunachira flows towards the Mababe Basin. The Thaoge, the most westerly distributary, drains in the direction of Lake Ngami and the central distributaries, the Mboroga and Jao, terminate at the Kunyere and Thamalakane Faults at the distal end of the delta. These faults then redistribute the water of the Mboroga and Jao distributaries towards Lake Ngami and the Mababe Basin via the Kunyere River and the two-directional Thamalakane River. Furthermore, there is an additional offtake via the Boteti River which drains towards Lake Xau and eventually the Makgadikgadi Pans (Figs. 2.4 & 2.7) (Thomas & Shaw 1991).

THE MABABE DEPRESSION

The Mababe Depression is a heart-shaped basin of about 90 km x 50 km and receives water from two possible inputs. Firstly, the Kwai River joins the Thamalakane River before it enters the Mababe at its southern end from the eastern side of the Okavango Delta Fan. Here, in the southern and lowest end of the basin, lies the Mababe Swamp (Burrough & Thomas 2008). The second input is via the Savuti Channel which is an offshoot of the Linyanti Swamp (Thomas & Shaw 1991). Water from this input may either be from the Zambezi River System or from both the Zambezi and the Okavango Systems. The Cuando River (Kwando in Botswana) originates in Angola, flows across the eastern Caprivi and then forms the border between Namibia and Botswana in a south-easterly direction. The Kwando River becomes the Linyanti River which flows east into the ephemeral Lake Liambezi, after which it is known as the Chobe River. The Chobe then connects to the Zambezi River. During years of exceptional flooding in the Okavango Delta, water flows along the Selinda Spillway (which is normally dry) into the Linyanti Swamp, connecting the Okavango and the Zambezi. In such an instance the water entering the Mababe Basin via the Savuti will have originated from both the Zambezi and the Okavango Systems (Fig. 2.4).

Although oral tradition supports the existence of ‘Lake Mababe’ in the eighteenth century, it has received little inflow and therefore has not been a standing lake for more than one hundred years. The recent (2009/2010) high flooding of the Okavango caused the Selinda Spillway to link up with the Linyanti Swamps (NASA Earth Observatory 2012a; 2012b), which connected the Okavango and the Zambezi Rivers for the first time in over 30 years. NASA Earth Observatory (2012a; 2012b) published satellite images taken in 2012 in which one can see the Savuti River filling the northern extremities of the Mababe Depression and forming the Savuti Swamp (Fig. 2.14).

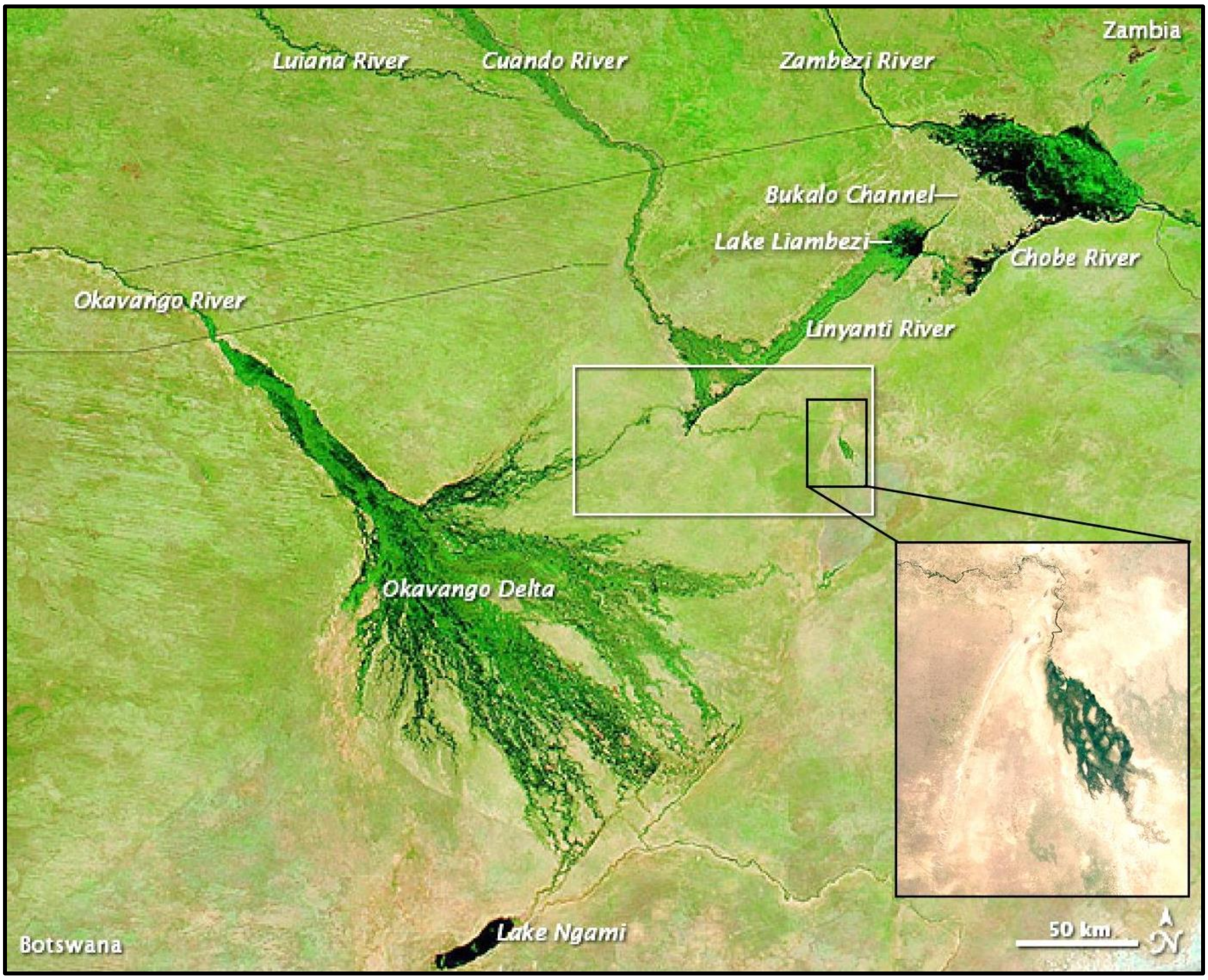

Figure 2.14: The Savuti Swamp. NASA satellite images indicate how the exceptional floods in the Okavango in 2009 and 2010 caused the Selinda Spillway to link up with the Linyanti Swamps, connecting the Okavango and Zambezi Rivers for the first time in over 30 years (Satellite images acquired from NASA Earth Observatory 2012a; b).

LAKE NGAMI

Livingstone and his companions were the first European travellers to visit Lake Ngami (Fig. 2.4) at its north-eastern end on 01 August 1849, at which time they described observing a "fine-looking sheet of water". During the 19th century, the most westerly distributary of the delta fan, the Thaoge River, used to be the major source to Lake Ngami. Today, Lake Ngami receives its water via two fault-controlled rivers - the Kunyere (Fig. 2.15A) and Lake (Fig. 2.15B) Rivers. The latter is also known locally as the Nghabe River. The Lake River receives its water from the

Thamalakane River (Fig. 2.15C) and meets up with the Kunyere at the village of Toteng (Fig. 2.7). The water then travels down a well-defined channel and eventually washes into Lake Ngami at its north-east extremity (Figs. 2.4 & 2.7) (Shaw 1983; 1985).

Shaw (1985) suggested that in the early 1850s Lake Ngami stood between 928 and 930 m on a seasonal basis and received water from two inputs. The first and major input from the Thaoge reached the lake by June and the second input from the Kunyere and Lake Rivers by August. Swamp-like conditions were created in the maze of channels north of Ngami and it is believed that, when full, the lake back-flooded the Lake River towards its confluence with the Thamalakane and Boteti Rivers (Fig. 2.4) (Shaw 1983; 1985).

From the mid-1850s onwards, however, the Thaoge's flow began to diminish in regularity and volume and ceased to flow completely between 1877 and 1881, at which point Lake Ngami dried (Shaw 1983; 1985). Associated with the drying of the Thaoge, and subsequently Lake Ngami, was an increase in flooding of the more eastern distributaries of the Delta: the Maunachira, Mboroga and Santantadibe (Wolski & Murray-Hudson 2006). This diversion of the Okavango's waters to the central swamp area may have been caused by tectonic activity, but the most likely cause is the blockage of the upper and middle Thaoge Channels by *Cyperus papyrus* (Shaw 1983; 1985).

Lake Ngami became a closed-system and received inflow from the Kunyere and Lake Rivers on a cyclical basis only. From 1881 to 1985, there were five periods during which the lake bed was dry for at least two consecutive years, which all coincided with a reduced flow in the feeder-rivers. During this century, maximum water levels, with water reaching between Sehitwa and Bodibeng, were attained in 1898-99, 1904, 1925, 1968-69 and 1978-79 (Shaw 1983; 1985). In the 1970s an area in the upper Mboroga dried which may have caused a reduction in flooding in the Santantadibe and Gomoti, but an increase in the Maunachira and Kwai Channels. By 1989, Lake Ngami received water for the last time until 2004 (Wolski & Murray-Hudson 2006).

In 2004, the lake received substantial inflow via the Xudum (which had been receiving proportionately more water since 1997) despite the fact that flow was not extensive in the other distributaries of the delta. The shift in flooding to the Xudum was at the expense of the Thaoge and not of the Boro. A change in the hydrological system of the Okavango Delta caused the shift in flooding, but it is unknown as to whether it was due to a tectonic event or an abrupt permanent vegetation change that may have created a new flow path and redirected the water (Wolski & Murray-Hudson 2006).

Since 2004, Lake Ngami received water seasonally, but not enough to fill the lake to more than a shallow pool (Figs. 2.15D & 2.15E). In 2010, however, unusually high rainfall in the catchment area in Angola caused an exceptional flood to travel down the length of the delta, filling Lake Ngami for the first time in 21 years (Fig. 2.15F). The high flood continued into the next two years and by 2012 Lake Ngami had filled to such an extent that it reached into the village of Sehitwa (Fig. 2.16A) and was inundated to the same maximum capacity that Shaw (1985) reported it to have been between 1880 and 1985. When travelling on Lake Ngami by boat water stretches to the horizon, as far as the eye can see (Fig. 2.16B). The Kunyere and Lake Rivers flooded their banks and bridges at Toteng and elsewhere had to be repaired (Figs. 2.15A & B). Along with the floods, uncountable fish washed into Lake Ngami from the floodplains of the Okavango (Figs. 2.16C & 2.16D) and in no time birds and other aquatic organisms had moved in (Figs. 2.16E & 2.16F), forming an instant ecosystem in an area that until recently was bone-dry. Between 2011 and 2014 Lake Ngami, as in the past, supported productive fisheries. This time, however, it was mostly commercial, chaotic and uncontrolled with hundreds of thousands of people camping along the shore, fishing and sending their catch to Angola as large blocks of pressed, dried fish (Figs. 2.17A-F). In 2015, however, the Botswana government put a stop to it and placed a total ban on fishing in the lake. This only caused people to move their activities to the Okavango Delta.

Figure 2.15: **A**: The Kunyere River in flood at the village of Toteng in August 2011. **B**: The Lake River (2011) flooded its banks, filling Lake Ngami. **C**: The Thamalakane River in Maun in August 2011. **D**: Lake Ngami as a shallow pool in October 2007. **E**: In December 2009 Lake Ngami had increased in size, but remained a shallow sheet of water. **F**: Aerial photograph of Lake Ngami inundated in August 2011.

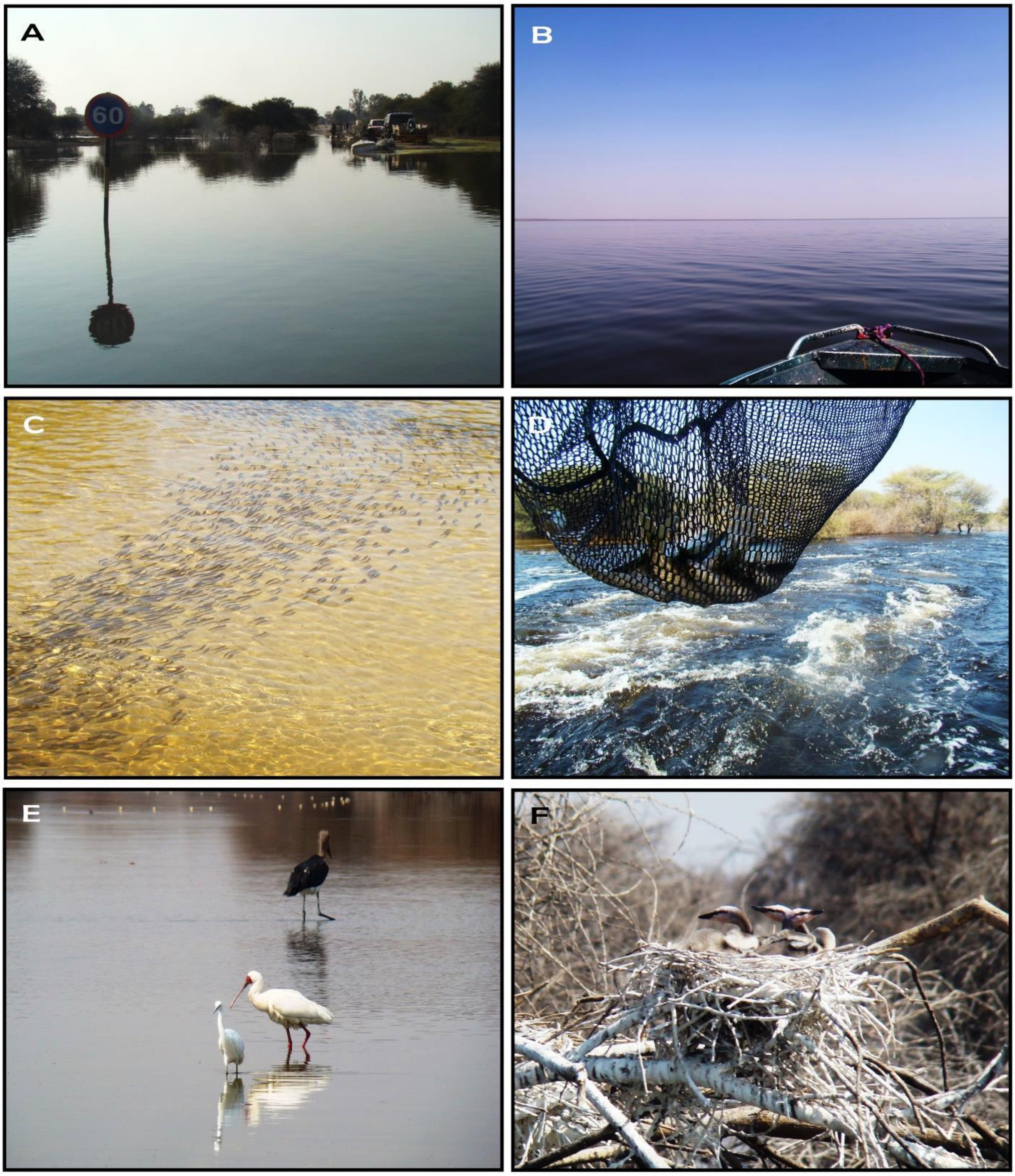

Figure 2.16: **A**: Lake Ngami washing into the village of Sehitwa in August 2012. **B**: By August 2012, Lake Ngami had filled to such an extent that water stretched to the horizon. **C** & **D**: In August 2011, the Okavango floods washed an uncountable number of fish into Lake Ngami via the Kunyere River. **E** & **F**: In no time, birds and other organisms had moved into Lake Ngami, creating an instant ecosystem.

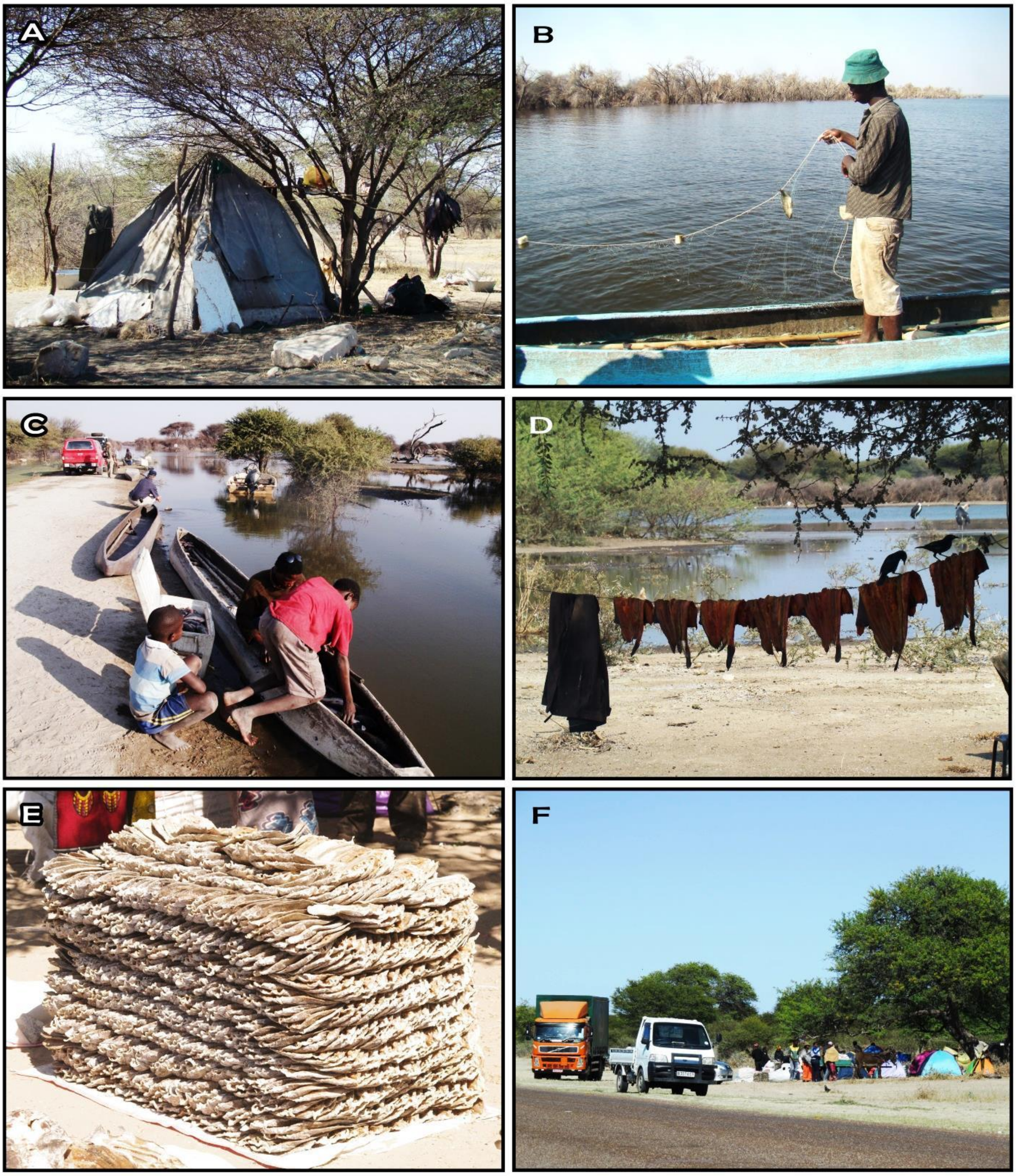

Figure 2.17: Since the inundation of Lake Ngami in 2010 it supported productive fisheries which sustained livelihoods, but unfortunately were mostly commercial, chaotic and uncontrolled. **A**: Thousands of people camped along the shore of the lake. **B** & **C**: Local fishermen removed their catch from their nets and brought it to the shore with mekoros (local dug-out canoes). **D**: The fish were hung on lines to dry. **E** & **F**: Large blocks of pressed, dried fish were sent to Angola.

Lake Ngami receives more than 80% of its water from the Okavango Delta, while the remainder is derived from local rainfall. Hence, the lake levels rise seasonally following the arrival of the Okavango floods, with a maximum inflow in August. Lake levels usually fall between October and May and seasonal variations can be as much as 2 m. Due to this regime, the lake is out of phase with local climatic conditions, as is the case with the delta. Peak levels are reached during the dry season and the variation of inflow does not reflect local climatic changes, but is dependent on fluctuations in the Cubango and Cuito Rivers as well as hydrological conditions within the Okavango Delta (Shaw 1983; 1985).

THE BOTETI RIVER, LAKE XAU AND MAKGADIKGADI PANS

The Thamalakane River at the distal end of the delta travels in two directions. It flows east towards the Mababe Basin and west towards Lake Ngami, but on its course towards Ngami, approximately 18 km south of Maun, the Thamalakane splits into two rivers – the Lake (Nghabe) River and the Boteti River (Fig. 2.18A). As previously mentioned, the Lake River eventually joins the Kunyere River and flows into Lake Ngami. The Boteti River, however, flows in a south-east direction and is the main inflow to the Makgadikgadi Basin (Fig. 2.4). The Boteti River is clearly a misfit as it has the carrying capacity of the full Okavango flow, yet most years its flow is not enough to reach the Makgadikgadi Basin (Thomas & Shaw 1991). Its bed is too wide and too deep to have been made by its recent meagre flow (Fig. 2.18B), which is a reminder of the more powerful river it used to be in the past (Ross 2003). Today, it carries a fraction of the Okavango's outflow a few hundred kilometres into the Kalahari (Fig. 2.18C) where it first fills Lake Xau before entering the Makgadikgadi Pans (Fig. 2.4). For millennia the Boteti has been a refuge in the dry season to the wildlife that inhabit the Makgadikgadi Pans and the central Kalahari Desert.

Lake Xau once was an impressive body of water, sufficiently fed by the Boteti, which is illustrated by the records of David Livingstone, who wrote about hunting sitatunga there in the mid nineteenth century (Ross 2003). Due to changes in rainfall patterns and prolonged drought in the mid-1980s, the Boteti River experienced a reduction in flow and by 1984 Lake Xau was completely dry (Sallu *et al.* 2010).

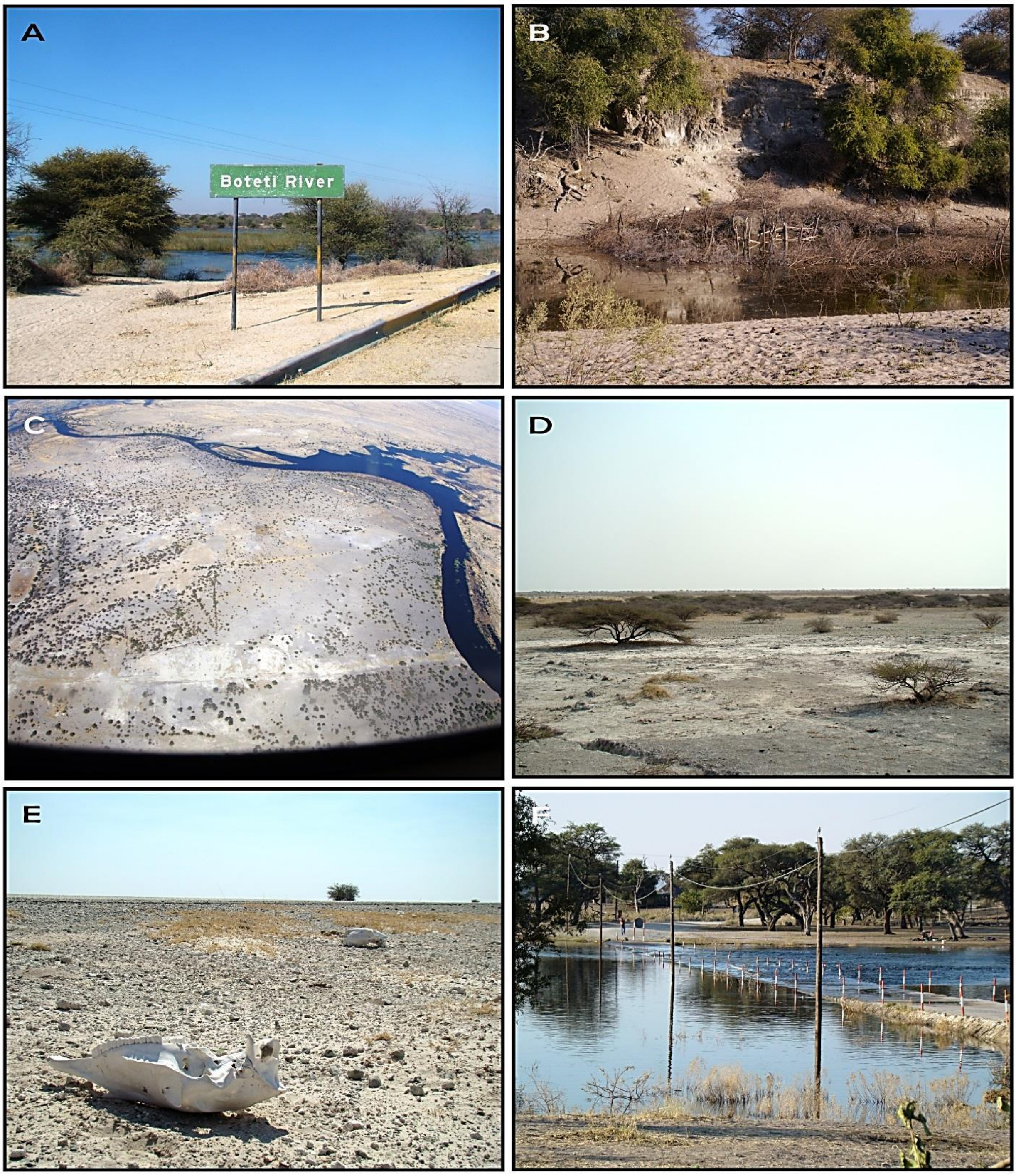

Figure 2.18: **A**: The Boteti River, August 2011. **B**: The Boteti River's wide and deep bed was an indication that it has carried volumes of water much larger than that which it carried before the 2010 floods. **C**: Arial image taken in August 2011 of the Boteti River flowing into the Kalahari on its course to Lake Xau. **D**: Since the early to mid- eighties, Lake Xau has been nothing but a bowl of dust. **E**: The remains of dead animals lie scattered in the extremely dry region of Lake Xau. **F**: The Boteti River in flood in August 2011 at the village of Rakops.

Since then it has been a bowl of dust (Fig. 2.18D), scattered by skeletons of animals that migrate to this traditional watering point just to find no water and are too weak to move on (Fig. 2.18E). Most often the outflow of the Okavango ends up as muddy pools in the Boteti, but the 2010 flood pushed the water deep into the Kalahari (Fig. 2.18C), so much so that the river reached full capacity, spilled its banks and washed away bridges in its path (Fig. 2.18F). In 2011 Lake Xau began to fill for the first time in about 30 years (Figs. 2.19, 2.20A, 2.20B & 2.20C) and by 2012 aquatic organisms had moved in and local communities were making use of the new resources. Floods, however, were not high enough to fill the entire lake and overflow into the Makgadikgadi Pans.

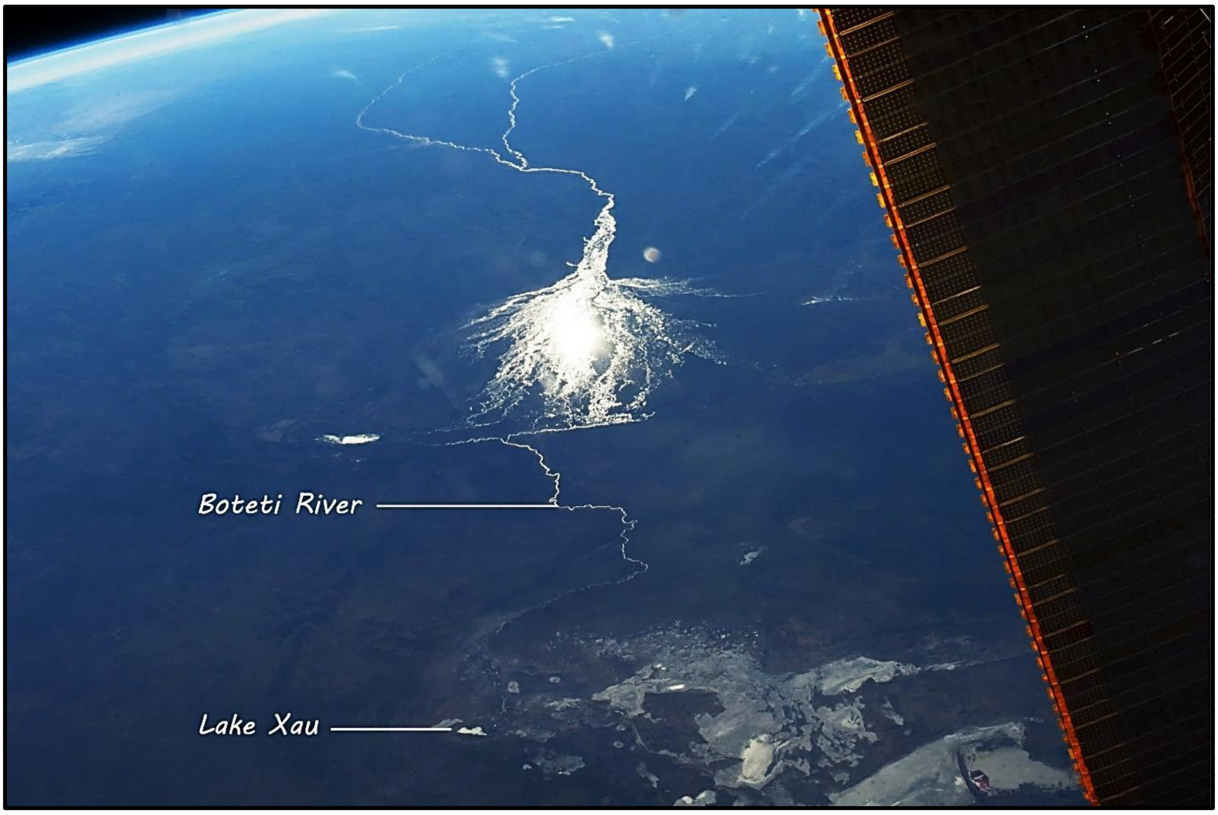

Figure 2.19: NASA satellite image (image acquired 6 June 2014) of the Okavango River and Delta, Lake Ngami, the Boteti River, Lake Xau and the Makgadikgadi Pans. The image shows water travelling down the Boteti River from the Okavango Delta and filling Lake Xau (Satellite image required from NASA Earth Observatory 2014).

The Makgadikgadi Basin is approximately 37,000 km² in size and contains a series of salt pans. To the west lies the larger Ntwetwe Pan and to the east Sua Pan, while a number of smaller pans lie to the west and south of Sua (Thomas & Shaw 1991). The Makgadikgadi Basin is the only one of the three lake basins that holds shallow, seasonal water on a regular basis. This water does not only originate from the Okavango, but also from other endoreic systems towards the east (Nash 1996; Burrough & Thomas 2008). One such river, which contains a seasonal flow and ends up in the Makgadikgadi Depression is the Nata River.

THE NATA RIVER

The Nata River (as it is known in Botswana) (Fig. 2.20D) or the Amanzanyama River of Zimbabwe helps to replenish aquifers and is an important source of life for the local people of the region. It flows off the Zimbabwe Plateau in a south-westerly direction and eventually enters Sua Pan. As is true for the entire Botswana, the climate in the region of the Nata is semi-arid. The rainfall is low, ranging between 240 mm and 700 mm and averaging 400-450 mm annually, and comes in the form of short, but intense, thundershowers. On the other hand, evaporation rates are high and at times may be as much as eight to ten times that of the rainfall input in the Kalahari. The wet season is from November to April, but rainfall in the area is very unpredictable and drought is a fairly common occurrence (Hitchcock & Nangati 2000; Hitchcock 2003).

The Nata River has a catchment of approximately 23,000 km², most of which is in Zimbabwe, and an annual flow of about 0.279 km³. This represents a significant resource by eastern Botswana standards (Hitchcock 1995; 2003; Hitchcock & Nangati 2000). The rivers in north-eastern Botswana and western Zimbabwe are ephemeral and the Nata River is the largest of these and has two smaller rivers as tributaries, namely the Dzivanini and Sa/a Rivers. Not only is the Nata seasonal, it also experiences long-term variations in flow. During some years when rainfall is high, the river may flow for extended periods, while on the other hand it may not flow at all, sometimes for several years, during periods of drought. These long-term climatic changes and droughts have significant impacts on the faunal, floral, livestock and human populations in the region (Hitchcock 2003).

Peak flow in the Nata is generally between January and March each year at which time it flows into its delta in Sua Pan. Large numbers of flamingo and other waterfowl congregate in a shallow lake (Fig. 2.20E), 400-600 km² in size, within the Nata Delta, to feed and breed (Hitchcock 1995; Hitchcock & Nangati 2000). Hence, the Nata Sanctuary was established in the late 1980's. It is a conservation area which covers 230 km², is located in the northern tip of Sua Pan and incorporates the southern part of the Nata River and what is known as its delta (Hitchcock 2003).

The lower reaches of the Nata contain brine pools in which salt of an extremely high quality is formed (Fig. 2.20F). In the past local people used to sell salt which they extracted in blocks from the Nata River. This important source of income has been halted, however, due to the establishment of the Nata Sanctuary. Today, people of the Nata River further upstream still use its water for domestic purposes such as drinking, personal hygiene and washing of clothes and dishes, as well as for construction purposes. They prefer not to collect drinking water from the pools in the river, but dig holes in the sand close by instead, allowing water to seep into these holes. The pools, however, are important sources of watering and grazing for livestock as well as for fishing (Hitchcock 2003).

Pans are scattered across the area which consists of gently rolling sandy plains. Most of the area is underlain by Kalahari deposits and the topography is slight (Hitchcock & Nangati 2000). Elevations decrease from 956 m above sea level at the point where the Nata enters Botswana from Zimbabwe to 910 m above sea level at the village called Nata (Hitchcock 1995; Hitchcock & Nangati 2000). It is an unusual river in that water flows relatively quickly downstream once rains in Zimbabwe have filled it, but because of its low gradient, the water currents sometimes reverse themselves and flow back upriver (Hitchcock & Nangati 2000; Hitchcock 2003). The area is so geologically dynamic that the slightest twist in the crust can redirect flow. It is no surprise then that the Nata is referred to as "the two-way river" by local communities.

Figure 2.20: **A**: Arial photograph of water entering Lake Xau in August 2011. **B**: The vanguard of water entering Lake Xau in 2011 after it had been bone-dry for about 30 years. **C**: Lake Xau, August 2011. **D**: The Nata River at the Nata Village, July 2012. **E**: Flamingos wading in the Nata Delta in Sua Pan. **F**: A brine pool in the lower Nata River containing crusts of salt.

THE ROLE OF MICRO-ORGANISMS IN THE WATERWAYS OF NORTHERN BOTSWANA.

The entire spectrum of wetlands and waterways in northern Botswana are of extreme importance, directly and indirectly, to the well-being of human populations in the area, the majority of whom live in poverty. Fortunately, once the ephemeral systems are inundated, instant ecosystems are created, which provide many services. Zooplankton, having diapausal life history stages, play an important role in the formation of instant ecosystems. Rotifers, for example, are known to produce resting eggs that are able to remain viable for more than 35 years, while cladocerans may produce resting eggs that can hatch after a number of decades. The diapausing eggs of calanoid copepods may remain viable for at least three years and most probably up to 15 years (De Stasio, Jr. 1990). These organisms are vital building blocks within the aquatic food chain and are important for secondary production, nutrient cycling and energy transfer, amongst others (Pace & Orcutt, Jr. 1981).

The flooding of the Okavango Delta and its associated basins in 2010 prompted a long, but exciting journey into the investigation of the zooplankton of northern Botswana.

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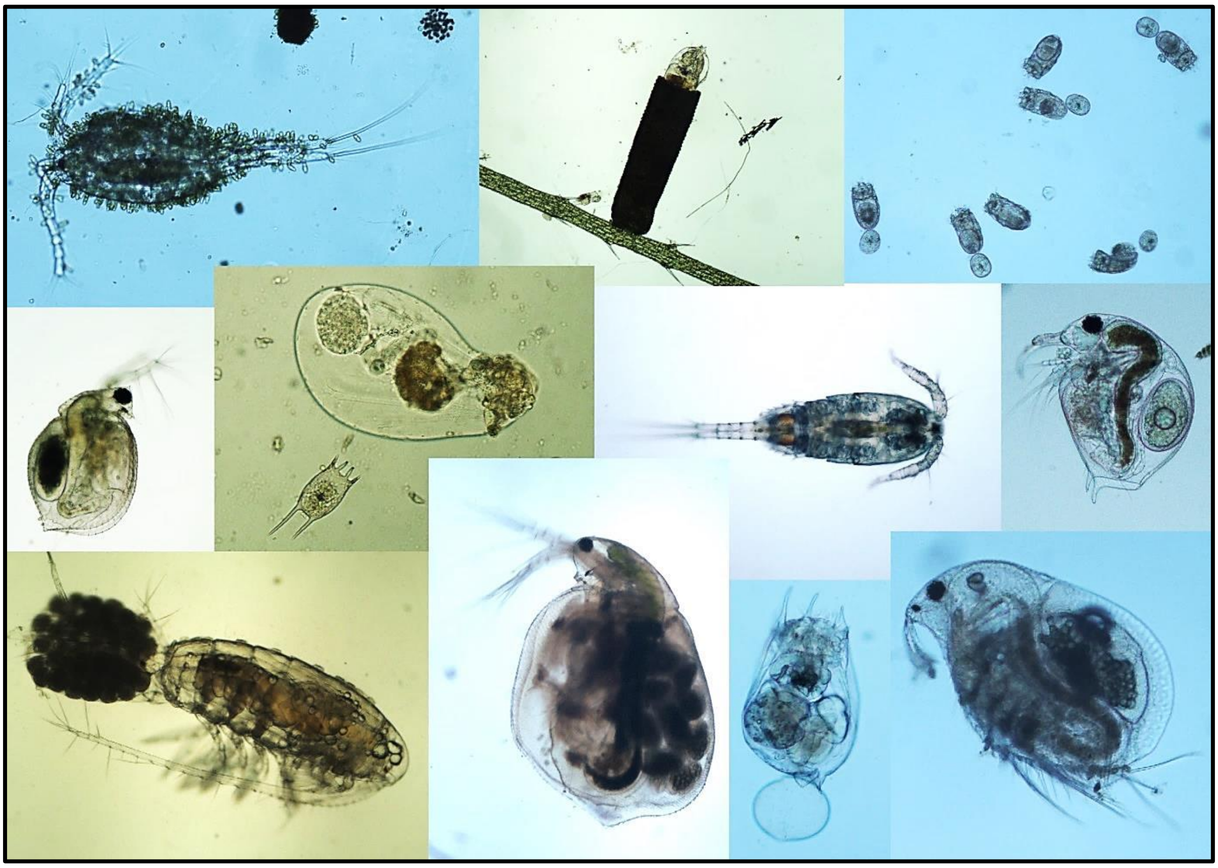
Chapter 3



FRESHWATER ZOOPLANKTON: AN OVERVIEW

INTRODUCTION

Zooplanktonic organisms are important in structuring phytoplankton communities and in facilitating energy flow to higher trophic levels in all aquatic environments (Barnett *et al.* 2007). Freshwater zooplankton mainly includes three major groups, i.e.: Protozoa, Rotifera and Crustacea. The freshwater micro-crustaceans further comprise three principal taxa, namely the ‘Cladocera’, Copepoda and Ostracoda, which have evolved an array of body forms and have colonised a high diversity of habitats, including every aquatic environment (Dole-Olivier *et al.* 2000). Protozoans are rarely included in freshwater zooplankton studies as they require different methods of sampling, which are normally not included in such surveys. Furthermore, rotifers and crustaceans (Cladocera and Copepoda specifically) are considered more important in terms of grazing, density, biomass, production and nutrient regeneration (Pace & Orcutt, Jr. 1981).

Although sampling was carried out to include all rotifers and microcrustaceans, focus was placed on the Rotifera, Cladocera and Copepoda for the purpose of the present study.

ROTIFERA

Rotifers were originally classified as Infusoria, mainly because of their conspicuous ciliation and their microscopic size, until Dutrochet (1812) became the first to regard the group as a biological unit and termed it Rotifera (Ruttner-Kolisko 1974). They are often referred to as “wheel-bearers” because of the synchronised beating of their ciliated head-crowns which look much like turning wheels (Figs. 3.1, 3.3 & 3.4). Rotifers are acoelomate worms which have many structural features in common with turbellarians, gastrotrichs and nematodes and range in length from about 40 µm to around 2 mm (Brain 2002).

Only a minor part of zooplankton biomass is made up of rotifers due to their minute size. The dry mass of an individual *Daphnia* Müller, 1785, for example, may equal that of between 300 and 500 rotifers (Ruttner-Kolisko 1974; Brain 2002). Nevertheless, they often occur in densities of up to 1000 individuals per litre and are ubiquitous, occurring in almost all types of freshwater habitats (Segers 2008). Rotifers play an important part in the production cycle since they have a rapid turnover rate and metabolism and many feed on bacteria and detritus, therefore, making them considerably independent of autotrophic production (Ruttner-Kolisko 1974; Brain 2002). Their high population turnover rates means that they are very sensitive to changes in water quality. Rotifer community structure allows for the estimation of pollution levels and can indicate changes in environmental conditions over time. They are considered to be useful indicators of water quality and trophic status and have for many years been used for chronic toxicity tests (Marneffe *et al.* 1998). The above-mentioned factors explain their standing, together with Cladocera and Copepoda, as one of the three main groups of freshwater zooplankton and as important organisms used in mass aquaculture (Segers 2008).

CLASSIFICATION

There are a number of different classification schemes for Rotifera in which the three basic groups (Seisonidea, Bdelloidea and Monogononta) are treated differently. In one method, the Monogononta are considered a class and the Seisonidea and Bdelloidea (having two gonads) are orders within the class Digononta. Another method separates the Seisonidea from the Bdelloidea and the Monogononta due to the unique anatomy and obligatory sexual reproduction of the former. In this case, the latter two groups are placed in the class Eurotatoria. Furthermore, some investigators rank rotifers as a class within the phylum Aschelminthes, while others consider Rotifera to be a Phylum (Wallace & Snell 1991). For the purposes of this investigation, rotifers were classified according to the system used by Brain (2002) and Segers (2008).

SYSTEMATICS

The Phylum Rotifera comprises two classes, the Digononta and Monogononta, with more or less 120 genera (Ruttner-Kolisko 1974; Brain 2002) and 1,800 (Brain 2002) to 2,000 (Wallace & Snell 1991) species world-wide. Molecular studies have indicated that the Acanthocephala, which have been considered a separate phylum of endoparasitic organisms, may actually also belong to the Rotifera. Due to limited modern, comprehensive studies and the lack of a fossil record, knowledge on the phylogeny of rotifers is restricted (Segers 2008).

CLASS: DIGONONTA

Members of the class Digononta can be distinguished by their paired ovaries and are divided into two orders, namely the Seisonidea and the Bdelloidea (Fig. 3.1) (Brain 2002). The former consists of a single genus, *Seison* Grube, 1861, which is one of the most unusual and poorly studied taxa of Rotifera. The males and females are of similar size and morphology and both sexes have paired gonads and a functional gut. Their coronas are much reduced and are not used for locomotion or feeding and the trophi are fulcrate. The ovaries of the females do not possess vitellaria (Wallace

& Snell 1991). Until recently, only two species had been recognised, *Seison annulatus* (Claus, 1876) and *Seison nebaliae* (Grube, 1859), which can clearly be differentiated from other rotifers in their life history and anatomical characteristics (Markevich 1993). Both species are found on the leptostracan crustacean *Nebalia* Leach, 1814 as ectoparasites, to some authors and epibionts to others (Markevich 1993; Brain 2002; Segers 2008). Sørensen *et al.* (2005) more specifically explain that *S. nebaliae* feeds exclusively on bacteria and, hence, is a commensal, while *S. annulatus* on the other hand seems to feed on the hemolymph and most probably the egg contents of its host, making it a parasite. In 2005, Sørensen *et al.* (2005) described a new species, namely *S. africanus* Sørensen, Segers & Funch, 2005 from Gazi Bay, Kenya. This species was collected between sea grass, but it has been hypothesised that it does live associated with a host. The authors continue to propose that the genus *Paraseison* Plate, 1887 be re-established and that *S. annulatus* becomes *Paraseison annulatus* (Claus, 1876).

The second order of Digononta, the Bdelloidea (Fig. 3.1), is normally found in fresh water and mosses and comprises 18 genera and more than 360 species (Wallace & Snell 1991). Segers (2008) stated that the order Bdelloidea contains 461 'species' which includes animals of unknown ecology and a single marine species. They possess an almost uniform morphology and males are unknown and have never been found, which implies that reproduction is by parthenogenesis only (Wallace & Snell 1991; Brain 2002). Bdelloid rotifers have paired ovaries (Fig. 3.1) with vitellaria, more than two pedal glands, ramate trophi and a corona of either two trochal discs or a modified ciliated field. Many bdelloids are able to shorten and lengthen their bodies by telescoping due to their vermiform shape and pseudo segmentation (Fig. 3.2). They are not usually caught in plankton nets as they mainly occur in sediments, among plant debris, on the surface of aquatic plants, in the capillary water films in soils, or on mosses. They may, however, be sampled with a plankton net in waters with dense aquatic vegetation (Wallace & Snell 1991).

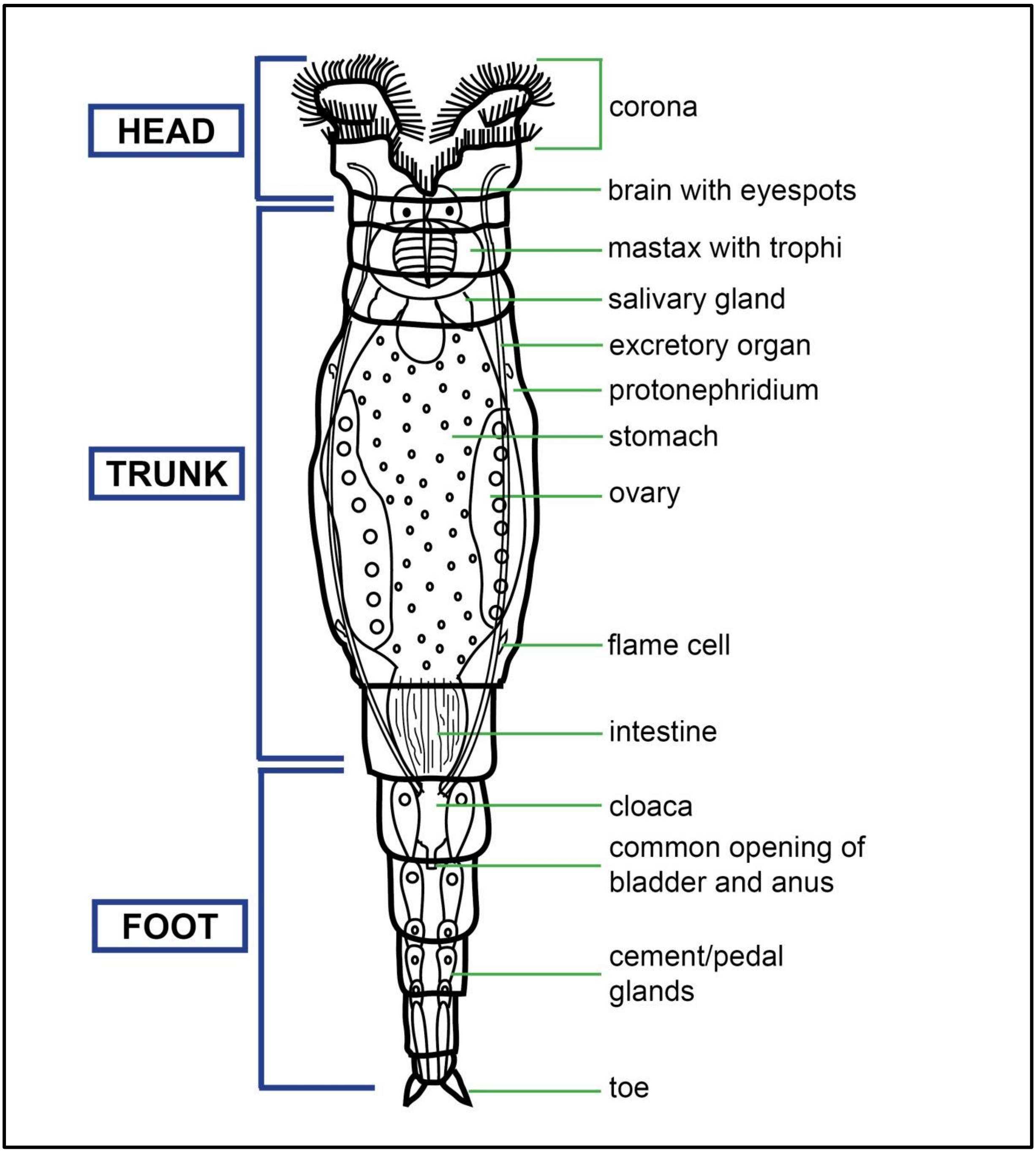


Figure 3.1: Diagram indicating the structure and anatomy of a typical female Bdelloidea rotifer (*Philodina* Ehrenberg, 1830), ventral view (Redrawn from Wallace & Snell 1991; Brain 2002).

Figure 3.2: Photomicrographs of Bdelloidea rotifers, *Rotaria neptunia* (Ehrenberg, 1830), from the Nata River, Botswana (August 2012). A number of bdelloids are able to **A**: shorten and **B**: lengthen their bodies by telescoping due to their vermiform shape and pseudo segmentation.

CLASS: MONOGONONTA

Members of the class Monogononta (Fig. 3.3) make up more than 80% of the known species of the phylum Rotifera and consist of three orders (Ploima, Flosculariacea and Collothecacea) (Brain 2002), 95 genera and more than 1,600 species (Wallace & Snell 1991). Segers (2008) suggested that the actual numbers may be much higher due to a lack of taxonomic knowledge and the occurrence of cryptic speciation amongst this class.

Monogononta are benthic, free-swimming or sessile and, as the name implies, females have single ovaries (with a vitellarium) (Fig. 3.3). Males are mostly tiny and structurally simpler (Fig. 3.4) and are only present in the plankton for a few days or weeks annually, but have not been observed for many species (Wallace & Snell 1991).

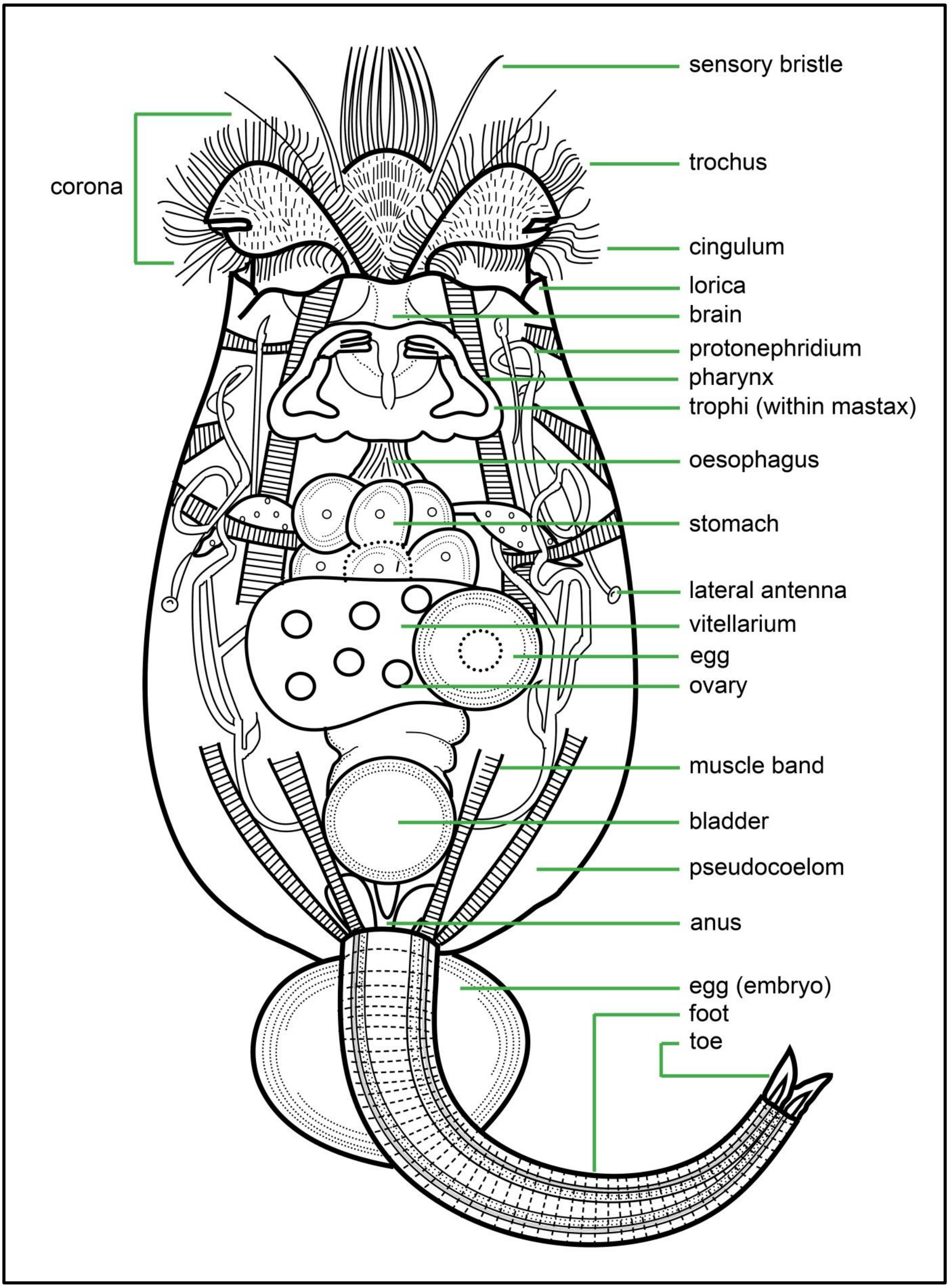


Figure 3.3: Diagram indicating the structure and anatomy of a typical female Monogononta rotifer (*Brachionus* Pallas, 1766), ventral view (Redrawn from Wallace & Snell 1991; Brain 2002).

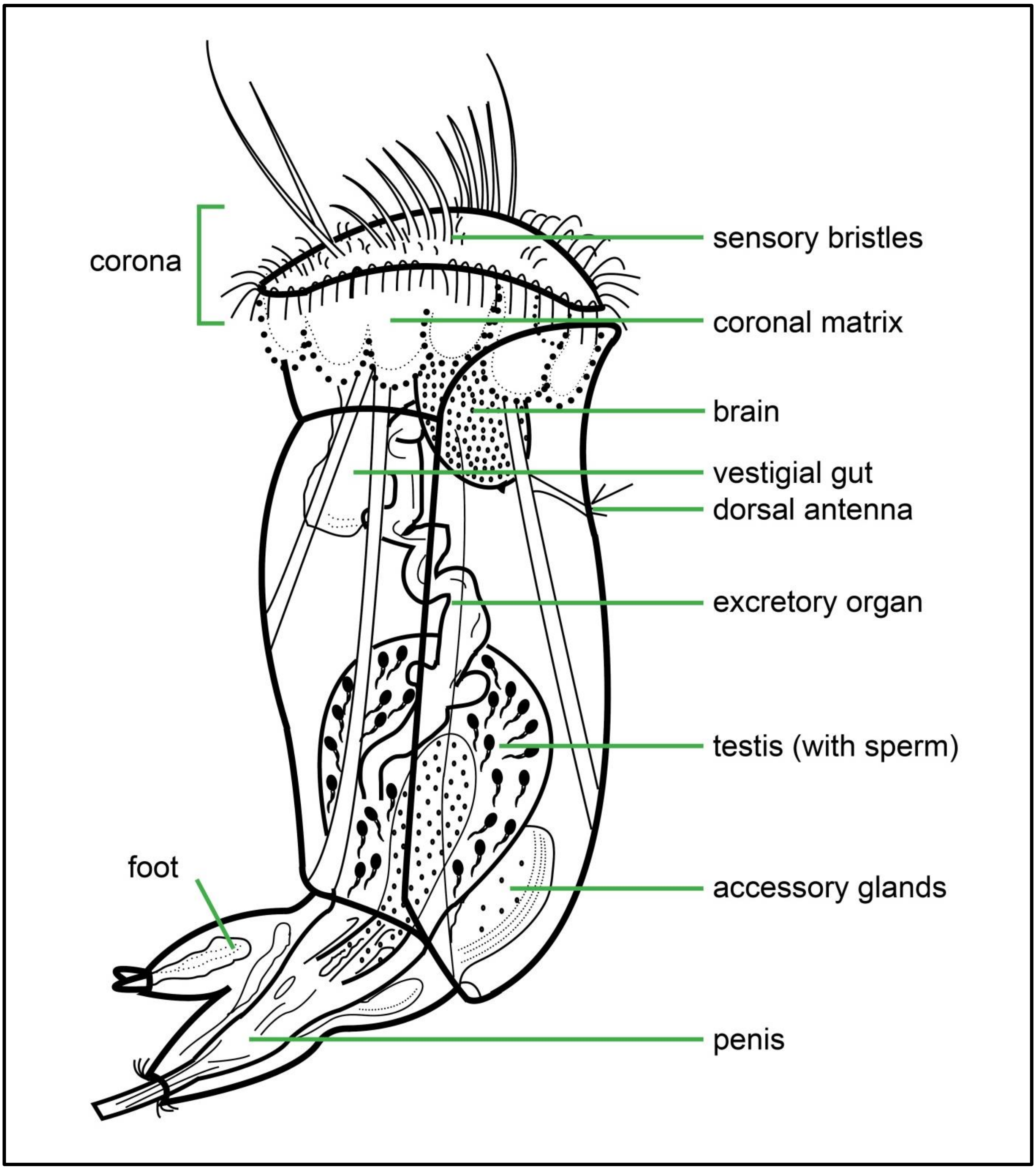


Figure 3.4: Diagram indicating the structure and anatomy of a typical male Monogononta rotifer (*Brachionus* Pallas, 1766), lateral view (Redrawn from Ruttner-Kolisko 1974; Wallace & Snell 1991).

MORPHOLOGY AND ORGAN SYSTEM FUNCTION

The body size of rotifers spans almost three orders of magnitude when one considers the different species (Stelzer 2005). Since rotifers are adapted to their environment and, hence, differ tremendously in their morphological features, descriptions in the present chapter will be based on simplified and generalised diagrams (Figs. 3.1, 3.3 & 3.4). The body of rotifers is typically comprised of three regions, namely: head (with corona), body/trunk and foot (Fig. 3.1) (Ruttner-Kolisko 1974; Brain 2002). Some authors (Wallace & Snell 1991) recognise a fourth body part, the neck.

HEAD

The head contains the tactile and optic sense organs, the oral aperture and the corona, a ciliated rotatory organ which is responsible for locomotion and bringing food to the mouth (Fig. 3.3) (Ruttner-Kolisko 1974; Brain 2002). The anterior ends of rotifers vary considerably in shape and a number of different types of corona have been described according to the distribution of cilia and the position of the mouth. In many rotifers, not all, the corona is made up of two ciliated rings, the trochus and cingulum, which are responsible for the production of water currents needed for feeding and locomotion (Wallace & Snell 1991).

TRUNK/BODY

The trunk cavity is filled with body fluid, as no circulatory system is present. It contains the digestive tract (which includes the pharynx, mastax, oesophagus, salivary glands, stomach, gastric glands and intestine), the excretory system (with flame bulbs, ducts and bladder), the genital organ (subdivided into the ovary and vitellarium), the brain and the longitudinal and circular muscles which extend into both the foot and the head (Ruttner-Kolisko 1974; Brain 2002).

Digestive System

After food is captured by the corona, it passes through a ciliated tube into a muscular pharynx and the mastax. On the inside, the mastax has a set of translucent jaws (chitinous lining) known as trophi. The trophi are important taxonomic features in rotifers and a number of different types have been identified based on the shape and size of the seven parts and the presence or absence of accessory parts (Wallace & Snell 1991). The different types of trophi are described in Ruttner-Kolisko (1974), Wallace and Snell (1991) and Brain (2002). Food is processed by the trophi in various ways, such as by grinding it, before it is swallowed via the oesophagus. Thereafter, food enters the stomach and the intestine before exiting via the anus in most species. In others, however, the gut ends in a blind stomach (Wallace & Snell 1991).

Excretory System

In all rotifers, a paired protonephridial system is responsible for excretion and osmoregulation. Usually they possess less than six flame cells, but larger rotifers may have up to 100. In most species, the tubules drain into a urinary bladder which leads to a cloaca, while in others the bladder is absent and a contractile cloaca adopts its function (Wallace & Snell 1991).

Reproductive System (females)

As formerly mentioned, members of the class Digononta (Seisonidea and Bdelloidea) have paired gonads and representatives of the class Monogononta have single gonads. Three units make up the reproductive organs of female rotifers; the ovary, vitellarium and follicular layer. The ovary and yolk-producing vitellarium are closely associated. The number of ovocytes in the ovary remains constant throughout the lifecycle, as do the nuclei in the vitellarium, making it a useful characteristic in the taxonomy of some species. Both units are surrounded by the follicular layer, which, in a few species, forms the oviduct. Commonly, rotifers are oviparous, releasing their eggs from the body for the embryo to develop on the outside, while only a few species are ovoviviparous and retain the embryo within the body until the offspring hatches. Amongst the oviparous, planktonic rotifers, some attach the egg to the mother’s body by a thin thread. Others attach the egg to substratum or release eggs equipped with floating devices into the plankton (Wallace & Snell 1991).

Nervous System

The nervous system consists only of a brain (cerebral ganglion), a few other ganglia and three types of sensory organs, namely mechano-, chemo- and photoreceptors. One or more photoreceptive eyespots (sometimes with a pigmented spot) are located in the anterior end, near the brain, in many species. Paired, ventral nerve cords, containing several other ganglia at the lateral nerve exit points, proceed along the length of the body from the brain into the foot (Wallace & Snell 1991).

Muscular System

The small group of longitudinal and circular muscles that make up the muscular system are inserted at a number of points on the integument or between the integument and viscera, while muscles are also present in the viscera. The corona and the foot are contracted by striated, longitudinal muscles which are also responsible for moving certain articulating spines. A number of species are able to jump as they possess powerful muscles which, when contracted, cause a downward sweep of their locomotory appendages (Wallace & Snell 1991).

FOOT

The junction between the trunk and the foot is marked by the anus which is the opening not only for the rectum, but also the bladder and oviduct (Ruttner-Kolisko 1974; Brain 2002). The foot is segmented and typically has two toes, but the number may vary between zero and four. It also has pedal glands, with outlets or ducts at the tip of the toes, which secrete a sticky cement for temporary attachment to substrata (Wallace & Snell 1991). Planktonic rotifers deviate to a large extent from the basic characters in terms of their body shape, their lorica and appendages and often in their anatomy. The deviations mostly have to do with a smaller or weaker foot and specialisation in feeding (Ruttner-Kolisko 1974).

CUTICLE

Rotifers have one of two types of body walls which cover their bodies and contain a filament layer called the intra-cytoplasmic lamina. The first type is a thin and flexible cuticle, while the second type is thickened and rigid and referred to as the lorica. The latter may be either rigid and sculptured or it may consist of a number of plate-like sections of the trunk cuticle. The thickness and flexibility of the body wall is, however, of little taxonomic importance (Wallace & Snell 1991; Brain 2002).

MALE MORPHOLOGY

Male monogonont rotifers are much smaller than the females and they have a very short lifespan. They usually do not feed as the digestive system is degenerate, in which case, the corona is used only for the purpose of locomotion. Male rotifers are fast and agile, characteristics which are necessary in their search for females (Brain 2002). They have a single, large testis (usually containing more than 50 mature, free-swimming sperm) which leads to the penis via a ciliated vas deferens. The latter has one, rarely two, pairs of prostate glands that discharge into it (Wallace & Snell 1991).

Apart from the normal sperm, males of some rotifer species possess rigid, rod-like atypical sperm near the aperture of the testis. It may be possible that it aids in copulation by piercing the body wall or by keeping the breach in the chemically dissolved body wall open (Ruttner-Kolisko 1974). The prominent penis, which is dorsal to the foot, penetrates the female's body wherever it is able to strike (Brain 2002).

REPRODUCTION

Rotifers reproduce only by means of eggs or live young and vegetative reproduction by proliferation does not occur as it commonly does in other primitive worms (Ruttner-Kolisko 1974; Brain 2002). The three basic groups of rotifers reproduce in different ways. Species in the order Seisonidea reproduce bisexually only. Gametogenesis occurs by meiosis and two polar bodies are produced. At the other extreme, male bdelloids are completely unknown and reproduction in this order is always asexual. Two equational divisions take place and two polar bodies are produced. Although males have not been described for a number of monogononts, it is generally assumed that most, or all, are capable of producing males for a few days or weeks annually, under the correct conditions. In other words, monogononts display parthenogenesis throughout most of the year, but sexual reproduction occasionally occurs (Wallace & Snell 1991).

CYCLICAL PARTHENOGENESIS AND MATING BEHAVIOUR

When monogononts reproduce in the absence of males by cyclical parthenogenesis it is known as the amictic phase, while the occasional sexual reproduction is called the mictic phase. Amictic (diploid) eggs are produced by amictic (diploid) females and by a single equational division they develop mitotically into females. As previously mentioned, most of the life-cycle of monogononts is spent in the amictic phase, but under certain conditions amictic females begin producing both mictic and amictic daughters, which do not differ morphologically and can only be distinguished by their offspring. The strength of the stimulus, which brings about the change, determines the proportion of mictic daughters produced and the duration of their production. Mictic females produce small haploid eggs via meiosis that, without fertilisation, develop into haploid dwarf males which swim faster and live shorter than females. If these haploid eggs are fertilised, however, they become diploid and develop into resting eggs with thick, often sculptured, highly resistant shells around the zygote (Ruttner-Kolisko 1974; Wallace & Snell 1991; Brain 2002; Schröder 2005).

Males, which are smaller and swim faster than females, do not have a functional foot and swim constantly without attaching to anything. Males and females swim randomly and the latter are passive in locating a mate and in reacting to the male once an encounter occurs. Males, on the other hand, display a distinct mating behaviour which only starts once the corona of the male has squarely contacted a female. Males are born with more or less 30 sperm and at each insemination they transfer two to three (Wallace & Snell 1991).

Resting egg production is maximised by male mating behaviour. Mictic females can only be fertilised for a short period after hatching, so males that copulate with older or amictic females are wasting their sperm. Males, therefore, initiate mating behaviour more often when encountering young females. In certain species, if males encounter female eggs, they attend it until the female hatches and then copulate with the new born. Interestingly, they do not attend male or resting eggs and are able to distinguish between female eggs which have just been deposited and more mature eggs which will hatch soon (Schröder 2005).

The vitellarium of females becomes a dark brown colour when they are about to produce resting eggs, making them easy to recognise. Resting eggs can often be used for identification as the shape, size and sculpturing is characteristic of the particular species (Ruttner-Kolisko 1974). These resting eggs are resistant to harsh environmental conditions, are able to survive such conditions for very long periods and may be dispersed over wide areas by wind, water and migrating animals. Periods of dormancy and hatching cues, which may include changes in light, temperature and salinity, are species- or even population-specific. The hatching cues or stimuli responsible for the onset of sexual reproduction are still poorly understood, with a few exceptions. When the resting eggs respond to hatching cues, diploid (amictic) females emerge, which enter into the asexual phase and complete the reproductive cycle (Ruttner-Kolisko 1974; Wallace & Snell 1991; Brain 2002).

In some populations of *Asplanchna* Gosse, 1850*, Conochilus* Ehrenberg, 1834 and *Sinantherina* Bory de St. Vincent, 1826 an unusual deviation of the monogonont life cycle has been observed. In a condition similar to what is found in cladocerans, some amphoteric female rotifers have the ability to produce both female (diploid) and male (haploid) eggs, while others may produce females and resting eggs or males and resting eggs (Wallace & Snell 1991).

Theoretically, resting eggs can accumulate to high densities in sediments (particularly on the surface), due to their capacity to remain dormant for extended periods (Wallace & Snell 1991). They do, however, not only sink into the sediment - very often they possess floating devices, are attached to other planktonic organisms or are washed ashore. It has been stated that most plankton species take three to six days to hatch after the stimulus for hatching has been applied. However, how sexual reproduction is caused in a succession of parthenogenetic generations has long exercised the minds of zoologists and to date has still not been completely resolved. Possible causes include changes in temperature, food supply, pH, chemical conditions or restriction of living space and must be unspecific, affecting the organisms through a general system such as their metabolism (Ruttner-Kolisko 1974). Schröder (2005) listed photoperiod, the uptake of α-tocopherol enriched food, crowding, temperature and salinity, amongst others, as the most important possible mixis-inducing factors. In my opinion, it is therefore extremely important to note the environmental conditions such as physical and chemical water quality parameters when sampling, not only for rotifers, but zooplankton as a whole.

ECOLOGY

Environments where organisms are able to survive, thrive and reproduce are prescribed by the physiological tolerances of each species. An environmental tolerance curve for a species indicates:

- the environmental ranges (upper and lower lethal limits) within which that particular species is able to survive and reproduce, as well as
- the environmental optimum for the species, which is the environmental conditions at which reproduction and survival are maximal.

Environmental tolerances or niche widths have been determined for only a few rotifer species and for certain environmental factors (Wallace & Snell 1991).

The effect of pH, for example, has received a lot of attention, but since hydrogen ion concentration is related to other chemical parameters in freshwater, the effect of pH only is of little value. Based on pH alone, rotifers can be placed into three broad groups, namely: alkaline species, acid species and species with an extensive range. Furthermore, it has been found that rotifers have a pH optima of seven (neutral) or below in oligotrophic waters and of seven or above in eutrophic waters (Wallace & Snell 1991).

Salinity plays a major role in determining rotifer species diversity and dominance and saline water bodies, in general, have a lower diversity than freshwater systems, i.e. increased salinity reduces species diversity (Green 1993). In saline ephemeral environments, the change in salinity throughout a season may determine which species emerge in a habitat. In other words, it shapes the recolonisation dynamics after an adverse event such as desiccation (García-Roger *et al.* 2008).

The majority of rotifers require oxygen concentrations above 1 ppm. Some, however, are able to tolerate anaerobic or near-anaerobic conditions for short periods, while others routinely live in oxygen-poor regions (Wallace & Snell 1991) such as the

Okavango Delta. These and many more, physical and chemical factors, along with food availability and predation, define rotifer niche boundaries.

Rotifers are found in a wide variety of aquatic environments, including those that are prone to periodic desiccation. Bdelloid rotifers overcome this problem by means of cryptobiosis (also termed anhydrobiosis and osmobiosis), a process by which they slowly dry out and come to life again when there is water once more. More specifically, the term cryptobiosis refers to a slow or hidden metabolism, while anhydrobiosis emphasises the loss of water through evaporation and osmobiosis stresses water loss through external osmotic pressure. The head and foot of bdelloid rotifers in the desiccated state are retracted into the trunk and they resemble a wrinkled barrel (Wallace & Snell 1991).

This desiccation-survival ability of rotifers has been known since 1702, when Van Leeuwenhoek experienced the rehydration of members of the phylum Rotifera he collected from the dry sediment of rain gutters. As many bdelloids inhabit ephemeral environments, cryptobiosis is a very significant phenomenon. It is critical to the survival of the organism that metabolic water loss proceeds gradually during desiccation. When the animal is in the cryptobiotic state, fine cell structure is retained (in a greatly altered manner), there is a 50% reduction in pseudocoel volume, cells and organs are condensed into a compact mass, and the cytoplasmic volume decreased, reducing the animal to between 25 and 30% of its original size. Bdelloids in the desiccated state may remain viable that way for more than 20 years and recovery from it may take place in 10 minutes or up to a few hours, depending on the environmental conditions. The survival of desiccated bdelloids may be negatively affected if there was a food shortage before drying out. Moist environments and high temperatures may also influence survival rates (Wallace & Snell 1991). However, very little is known about the ecology of bdelloid rotifers, mainly due to the fact that they can only be identified while alive and need to be examined while feeding and creeping (Segers 2008).

Monogonont rotifers lack the process of cryptobiosis, but do form resting eggs when conditions are unfavourable (Brain 2002). This process has been described in detail above (see *Reproduction: Cyclical Parthenogenesis*). Brain (2002) stated that both desiccated bdelloids and monogonont resting eggs are dispersed in a number of ways, including being blown about by wind and, hence, many rotifer species are cosmopolitan and found wherever conditions are suitable (Brain 2002). Wallace and Snell (1991) seem to differ in their opinion. They stated that there is sufficient data to discredit the conclusion that passive dispersal successfully ensures the global distribution of most species. Wallace and Snell (1991) pointed out that Green (1972) demonstrated a latitudinal zonation in some planktonic rotifers and that Pejler (1977) showed the restricted distributions of a number of species. Furthermore, in several genera such as *Keratella* Bory de St. Vincent, 1822, *Notholca* Gosse, 1886 and *Synchaeta* Ehrenberg, 1832 endemism is relatively common. They stress that, while some rotifer species may be cosmopolitan, many are not and Dumont (1983) suggested that the current biogeography of rotifers was determined by continental drift and Pleistocene glaciations.

Furthermore, rotifers are not even uniformly distributed in water bodies. They display substantial variability in their horizontal and vertical distributions. This is mainly because water bodies are not unvarying habitats. Biotic factors (e.g. food availability and predators) and abiotic factors (e.g. dissolved oxygen concentration, light intensity, temperature and water currents) may vary significantly from one region to the next within a water body. Biotic and abiotic factors aside, distributions patterns within a water body may also be influenced, to a lesser degree, by locomotory behaviour, such as daily (diel) vertical migration in the water column. At night they usually come to the surface and exploit algal resources, while they avoid near-surface, visual predators, such as fish, during the day. The diel migrations of rotifers are never as dramatic as those of micro-crustacean zooplankton (Wallace & Snell 1991).

Rotifers mostly prefer fresh water, but in southern Africa, a number of species (particularly belonging to the genera *Brachionus* Pallas, 1766 and *Hexarthra* Schmarda, 1854) have been collected from brackish water sources. In the Namib Desert, *Proales similis* de Beauchamp, 1908 was found in springs with salinities almost three times that of seawater. Furthermore, a marine species of *Synchaeta* has been described from the south-western Cape, South Africa (Brain 2002).

More or less 30% of all rotifer genera live constantly or occasionally in the plankton where densities quite often reach 200-300 individuals per litre and on occasion may be as high as 1,000 individuals per litre. Densities of up to 5,000 individuals per litre have been recorded where sufficient food is available (Ruttner-Kolisko 1974; Wallace & Snell 1991; Brain 2002).

The following are the chief adaptations of rotifers to planktonic life, as listed in Ruttner-Kolisko (1974) and Brain (2002):

- They possess a reduced lorica (e.g. *Brachionus calyciflorus* Pallas), have an inflated body (*Asplanchna, Synchaeta*) or produce gelatinous material (*Conochilus, Collotheca* Harring, 1913*, Gastropus* Imhof, 1898) which all result in a lowered specific weight.
- Organs for attachments are reduced, which may include the total loss of the foot and toes (most planktonic forms) or just a significant shortening of the foot (*Synchaeta, Epiphanes* Ehrenberg, 1832).
- Appendages suitable for swimming and floating develop, such as bristles for skipping (*Filinia* Bory de St. Vincent, 1824, *Hexarthra, Polyarthra* Ehrenberg, 1834) or rigid spines (*Keratella, Kellicottia* Ahlstrom, 1938).
- Eggs are protected against sinking by attachment to the mother (*Brachionus, Filinia, Keratella*) or by possessing floating devices such as oil droplets (*Polyarthra*) or spines (*Synchaeta*) or by viviparous reproduction (*Asplanchna*).
- Individual rotifers link up in chains enabling them to float (*Hexarthra*).

Most rotifers are solitary, but a number of monogonont species, in eight genera, form permanent colonies (Wallace 1987).

COLONIALITY

A colony may be defined as a fairly stable group of individuals which occur in higher numbers than expected based on a number of factors such as temperature, light, food and shelter. Members of a colony are in direct contact with one another by body, tubes or gelatinous secretions and there is a high level of coordination among individuals. Given the close proximity of colonial individuals, competition for food may become so intense that it does not seem feasible for coloniality amongst rotifers to ever have evolved. It is, however, an evolutionary stable strategy as research has indicated that it provides advantages such as increased feeding ability, improved defence, increased inter-specific competitive ability and enhanced breeding capacity to its members (Wallace 1987). The formation of colonies is an extremely successful protective strategy in the genus *Conochilus*. It has been found that the colony size changes seasonally in relation to the size of the maxilliped of the predatory calanoid present during the season it was preyed upon (Brandl 2005).

All colonial rotifers belong to the families Flosculariidae and Conochilidae, reproduce in a fashion typical of monognonts and are not predators. More or less 70% are sessile, while three genera (*Chonochilus, Lacinularia* Schweigger, 1820*, Sinantherina* Bory de St. Vincent, 1826) have planktonic forms. Colonies do not reproduce by branching or budding, there are no specialised zooids and there are no connections between individuals, meaning that resources are not redistributed in the colony. The size of colonies may range from two to more than 1,000 individuals and may vary considerably in colonies formed by those species capable of creating large colonies (Wallace 1987).

Basically, coloniality is an adaptive strategy in the phylum Rotifera and may be explained in terms of energy efficiency and predator avoidance. Through increased feeding efficiency, it seems to increase the amount of usable energy for each individual. Furthermore, it provides protection from other invertebrate and maybe even vertebrate predators (Wallace 1987).

ROTIFERS OF THE OKAVANGO AND ITS ASSOCIATED BASINS

Green (2003) conducted a survey on the planktonic and periphytic rotifers of the Okavango Delta in 1992 as part of the IUCN review of the Southern Okavango Integrated Water Development Project. His study sites included a small lagoon off the main channel at Sepopa in the panhandle, as well as stations in the Lower Boro, Thamalakane and Boteti Rivers. Other studies which reported on the Rotifera of the Okavango Delta as part of zooplankton fauna include Cronberg *et al*. (1995), Hart (1997) and Siziba *et al.* (2011a). These results are summarised, discussed and compared to that of the present study in **Chapter 5**. Data is not available for the Rotifera of the Upper Panhandle, Lake Ngami, Lake Xau and the Nata River.

CLADOCERA

Information on the superorder Cladocera dates back to the 17th century (Forró *et al.* 2008), but it was originally recognised as a taxon by Latreille in the early 1800s and since then various internal changes have been made in the arrangement of its component parts (Fryer 1987a). Members of the superorder Cladocera are branchiopod crustaceans, commonly known as “water fleas”, and embrace a diversity of organisms which range from about 0.2 to 6.0 mm in length. They are primarily freshwater inhabitants and occur in pelagic, benthic and littoral zones (Forró *et al.* 2008). Cladocerans are at the same time one of the most successful groups of organisms in inland waters as well as a relict group. The small number which survive today are ‘living fossils’ as a number of extant genera thrived in the Early Mesozoic (248 to 65 million years ago) or earlier (Korovchinsky 2006). Anderson *et al*. (2004) described crustaceans similar to the cladocerans from as early as the Early Devonian (417 to 354 million years ago). It is most likely that the appearance of cladocerans in inland waters accorded with the initial faunas in the Carboniferous (354 to 290 million years ago) (Korovchinsky 2006).

Cladocerans are easily cultured, have a short generation time and reproduce offspring which are clones of the mother and hence are model organisms in basic and applied research. They have gained economic importance due to their use in aquaculture and large planktonic, filter-feeders have an indirect economic impact due to their phytoplankton-controlling ability and their importance as fish food. More importantly, however, they are significant components of freshwater fauna, particularly in the food web of stagnant waters. Human-mediated dispersal has allowed some species to successfully invade other continents and this trend will likely increase. On the other hand, a loss of habitat, and especially of temporary waters, may lead to a decrease in diversity or even the extinction of local species (Forró *et al.* 2008).

There has been much debate about the correct classification of the four main groups of Cladocera and to date no clear classification system is available.

CLASSIFICATION AND SYSTEMATICS

Fryer (1987a) questioned the validity or monophyletic status of the superorder Cladocera and stated that, in his opinion, the differences between the Ctenopoda, Anomopoda, Onychopoda and Haplopoda are sufficient to merit that they be separate orders of equal status to other branchiopod orders. Referring to the taxon as the 'so-called Cladocera', he stressed that the term Cladocera embraces a diversity of organisms and that the name should be rejected. In that same year, Fryer (1987b) presented a comprehensive review of former classifications of the class Branchiopoda and also proposed a new scheme in which he removes the 'so-called Cladocera' and elevates the four lower categories amongst them to ordinal rank.

A number of authors thereafter challenged Fryer's (1987a; b) classification (Negrea *et al.* 1999) and in 1999, Negrea *et al.* (1999) completed Fryer's (1987b) review by presenting the classification of Starobogatov (1986) which is not widely available and was overlooked by Fryer (1987b). Negrea *et al.* (1999) also proposed a new phylogenetic classification in which the Cladocera were classified as summarised in Table 3.1. Due to a large number of derived traits unique to the order Haplopoda, the authors separated this order from the other three cladoceran orders (Ctenopoda, Anomopoda and Onychopoda) and placed it in a superorder (Leptodorida) on its own. The remaining three orders were placed under the superorder Cladocera (Table 3.1). Some authors (Dole-Olivier *et* al. 2000; Forró *et al.* 2008) still make mention of four Cladoceran orders, but whatever their taxonomic position, it is imperfectly known.

For the purposes of this investigation, cladocerans were classified according to the system used by Forró *et al.* (2008) (Table 3.2). Despite the important new view that the Cladocera is an 'artificial taxon' (Korovchinsky 1996), the term remains useful and convenient and will here forth be used as a collective term for the branchiopod orders Anomopoda, Ctenopoda, Haplopoda and Onychopoda.

Table 3.1: Phylogenetic classification of the group of organisms known as Cladocera as proposed by Negrea *et al.* (1999).

Superclass Crustacea Lamarck, 1801
Class Branchiopoda Latreille, 1817 (as defined by Calman, 1909)
Superorder Leptodorida *
Order Haplopoda Sars, 1865
Family Leptodoridae Lilljeborg, 1861
Superorder Cladocera Milne-Edwards, 1840
Order Ctenopoda Sars, 1865 (=Sidoidea Baird, 1850, emend. Brooks, 1959)
Family Sididae Baird, 1850 (emend. Sars, 1865)
Family Holopedidae Sars, 1865
Order Anomopoda Sars, 1865 (=Chydoroidea Dybowski & Grochowski, 1894, emend. Brooks, 1959).
Family Daphniidae Straus, 1820 (emend. Sars, 1865)
Family Bosminidae Baird, 1845 (emend. Sars, 1865)
Family Ilyocryptidae Smirnov, 1976
Family Eurycercidae Kurz, 1875
Family Sayciidae Frey, 1967
Family Chydoridae Dybowski & Grochowski, 1894 (emend. Stebbing, 1902)
Family Ophryoxidae Smirnov, 1976
Family Acantholeberidae Smirnov, 1976
Family Macrothricidae Norman & Brady, 1867
Family Neothricidae Dumont & Silva-Briano, 1998
Order Onychopoda Sars, 1865 (=Polyphemoidea Baird, 1845, emend. Brooks, 1959)
Family Polyphemidae Baird, 1845
Family Podonidae Mordukhai-Boltovskoi, 1968
Family Cercopagidae Mordukhai-Boltovskoi, 1968

*As proposed by Negrea *et al.* (1999)

Table 3.2: Cladoceran orders and families as well as number of genera and species currently known in the Afrotropical geographic area and worldwide. Numbers in parentheses = endemic species. Summarised from Forró *et al.* (2008).

Taxa	**Afrotropical**		**World**	
	Genera	**Species**	**Genera**	**Species**
Order Anomopoda	36(1)	125(24)	76	537
Family Daphniidae	5(0)	25(1)	5	121
Family Moinidae	2(0)	10(1)	2	29
Family Dumontiidae	0	0	1	1
Family Ilyocryptidae	1(0)	8(3)	1	28
Family Bosminidae	2(0)	3(0)	2	14
Family Acantholeberidae	0	0	1	1
Family Ophryoxidae	0	0	2	3
Family Macrothricidae	5(0)	12(2)	11	60
Family Neothricidae	0	0	1	3
Family Eurycercidae	1(0)	1(0)	1	8
Family Chydoridae	26(1)	66(17)	49	269
Order Ctenopoda	4(0)	9(0)	8	50
Family Holopediidae	0	0	1	3
Family Sididae	4(0)	9(0)	7	47
Order Haplopoda	0	0	1	1
Family Leptodoridae	0	0	1	1
Order Onychopoda	0	0	10	32
Family Polyphemidae	0	0	1	2
Family Podonidae	0	0	7	17
Family Cercopagidae	0	0	2	13
Total	46(1)	134(24)	95	620

In his revision of cladoceran species listed in identification books, as well as in descriptions of new species, Korovchinsky (1996) found that there are around 568 species in eight families, but that very few species may be regarded as valid or fair. Unsurprisingly, Africa has the smallest number of valid and fair species (Korovchinsky 1996). Later papers identify higher species and family counts. Negrea *et al.* (1999) list 16 cladoceran families (including Leptodoridae of the order Haplopoda). Dole-Olivier *et al.* (2000) state that the four recognised orders contain 11 families and between 450 and 600 species (2% of which are marine). In their revision of the global diversity of freshwater Cladocera, Forró *et al.* (2008) list 17 families, 95 genera and 620 species worldwide (Table 3.2), but point out that this diversity underestimates the reality and that even higher-ranked taxa, such as the family Dumontiidae (Santos-Flores & Dodson, 2003) are still being discovered. Furthermore, there may be extensive cryptic diversity amongst some of the currently-recognised widespread species. The status of some species is vague and a number of them are probably such cryptic complexes. Only between 40 and 50% of species are valid and well-described (Forró *et al.* 2008).

All orders, families and local faunas of Cladocera worldwide have been insufficiently studied. The validity of many European species is acceptable as these were the first to be studied amongst the Cladocera. However, they have often been recorded from other countries based on incorrect identification and the belief that they are cosmopolitan (Korovchinsky 1996). Korovchinsky (1996) stated that even in Europe, where cladocerans have been studied most extensively, one cannot be sure of an identification as many descriptions are inadequate and closely-related species may co-exist.

Efforts in the taxonomy, systematics and global species richness of cladocerans have increased in the Neotropics and Asia and decreased in Europe and North America, but have always been poorly studied on the African continent (Van Damme *et al.* 2013).

MORPHOLOGY (Fig. 3.5)

Most cladocerans (Fig. 3.5) (Ctenopoda and Anomopoda) possess a bivalved, unhinged carapace which encloses the trunk and appendages. The anterior part of the body or head is not enclosed by the carapace (Seaman *et al*. 1999).

HEAD

The head protrudes from the body and is often produced to form a rostrum between small, uniramous antennules. The antennas, on the other hand, are large, biramous (excluding *Holopedium* Zaddach, 1855 females), segmented and branched (Seaman *et al*. 1999; Forró *et al.* 2008). They are situated near the posterior margin of the head and have a basal segment as well as two segmented rami. The antennas are the primary organs of locomotion and limnetic forms possess plumose setae which aid in swimming (Seaman *et al*. 1999).

A single compound eye and ocellus (anterior or ventral to the eye) are present (Seaman *et al*. 1999; Forró *et al.* 2008). The eye consists of a mass of pigment cells, surrounded by a number of lenses, and is continuously moved by muscles attached to it. The eye movement appears to be for orientation relative to incident light. Small, simple mouthparts are well hidden at the junction between the head and the body. These consist of a pair of sclerotised mandibles (most obvious), an upper lip or labrum, one pair of maxillae and a labium. It is uncertain as to what the function of the pores on the surface of the head is, but they are of taxonomic value in families such as the Chydoridae (Seaman *et al.* 1999).

BODY

The shell or carapace, which consists of two valves, encloses the body and forms a brood chamber on the dorsal side into which eggs are laid (Seaman *et al*. 1999). Four to six pairs of leaf-like thoracic appendages are mostly similar in shape in orders such as the Ctenopoda, Onychopoda and Haplopoda, but are greatly modified amongst the Anomopoda (Forró *et al.* 2008) for various functions such as food gathering and clinging to substratum (Seaman *et al.* 1999).

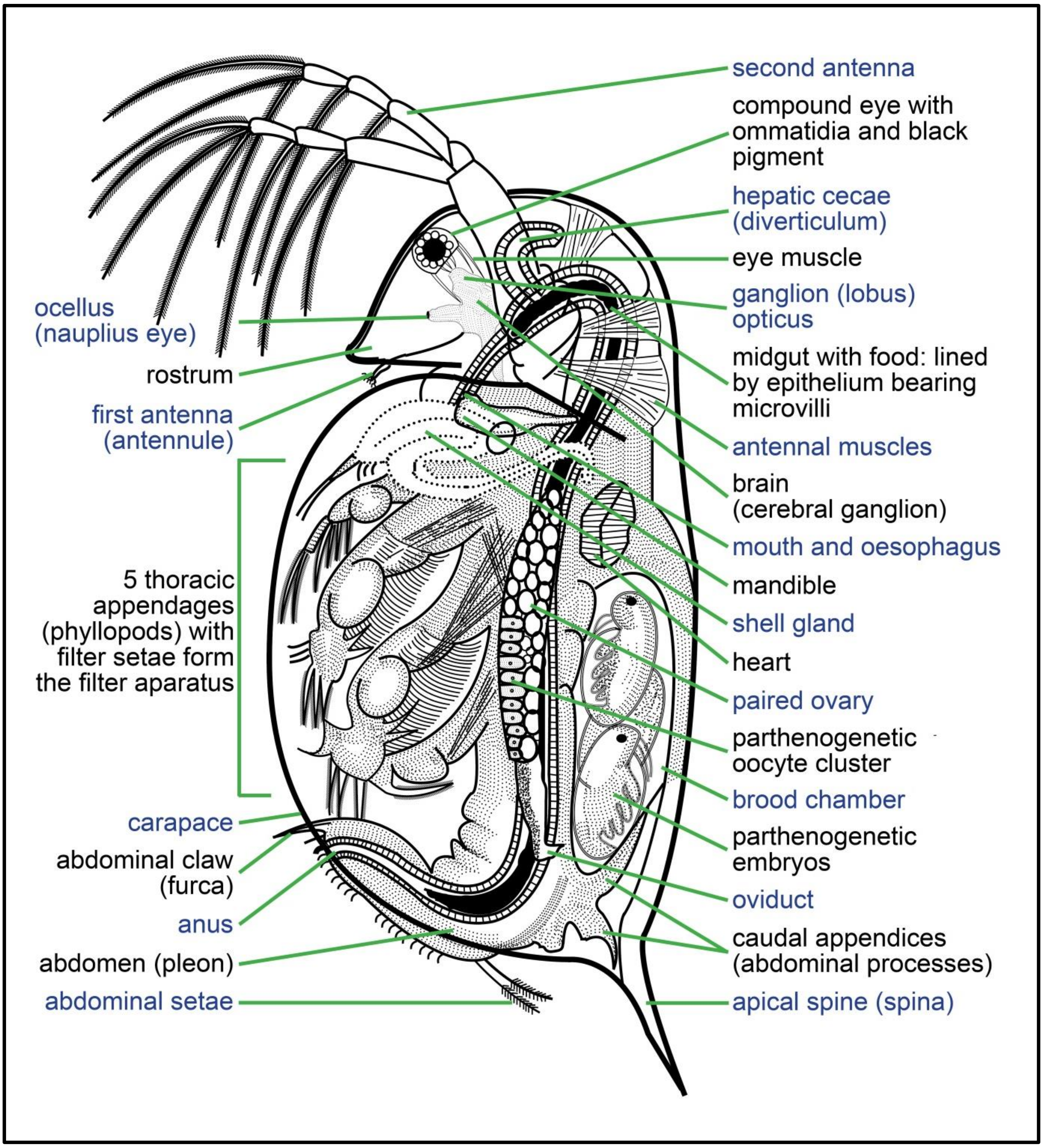


Figure 3.5: Diagram indicating the structure and anatomy of a typical adult female cladoceran (*Daphnia* Müller, 1785) with parthenogenetic embryos in her brood chamber (Redrawn from Ebert 2005).

Cladocera have a characteristic post-abdomen which bears two terminal claws and two abdominal setae on its dorsal side. Spines and teeth of various sizes and arrangements are present on the concave side of the abdominal claws. Basal spines are a few large spines near the base of the claw. The greater part of the claw is said to be denticulate when minute spines of the same size are present along its length. The pecten (comb) refers to a group of intermediate spines, if present, between the distal denticulation and basal spines. Anal spines are present in rows on the post-abdomen, but certain families lack these spines. Cladoceran intestines are simple and in a number of species, one or two digestive hepatic caeca protrude into the head area from the gut (Seaman *et al*. 1999).

MALE MORPHOLOGY

Most cladoceran individuals are females as males are absent from some populations or occur only at particular times. Generally, males are much smaller in size than females, have larger antennules, a shorter rostrum and hooked first legs (Seaman *et al*. 1999).

CYCLOMORPHOSIS

Cyclomorphosis refers to the ability of individuals or populations to seasonally change their shape or undergo allometric shifts. Members of the superorder Cladocera, amongst other planktonic organisms, are able to undergo seasonal cyclomorphosis, typical attributes being an enlarged spine and a change in the shape of their heads (Seaman *et al*. 1999; Lindholm 2002). An extensive literature documents cyclomorphosis in the cladoceran genera *Daphnia* Müller, 1785 and *Bosmina* Baird, 1845 and it seems as though it is primarily induced by the presence of invertebrate and fish predators (Lindholm 2002).

Reports on the phenomenon from warmer regions are uncommon and it seems more characteristic of cold-temperate zones (Seaman *et al*. 1999; Lindholm 2002). Seaman *et al.* (1999) stated that it had not been reported from southern Africa, but that considerable variations have been found within some species. Green (1967) recorded *Daphnia lumholtzi* Sars, 1885 with enlarged helmets from Lake Albert in Uganda and Rayner (1981) observed the same phenomenon in *Diaphanosoma excisum* Sars, 1887 from Lake Midmar, South Africa. Lindholm (2002) recorded

Daphnia laevis Birge, 1879 exhibiting traits of cyclomorphosis (regarding tail-spine length and helmet size) from the Okavango Delta, Botswana. Differences in tail-spine length and helmet size were also recorded in *Daphnia laevis* populations in the Okavango Delta during the present study. Populations sampled during August 2011 exhibited traits of cyclomorphosis, while those sampled in August 2012 did not (Figs. 3.6A & 3.6B).

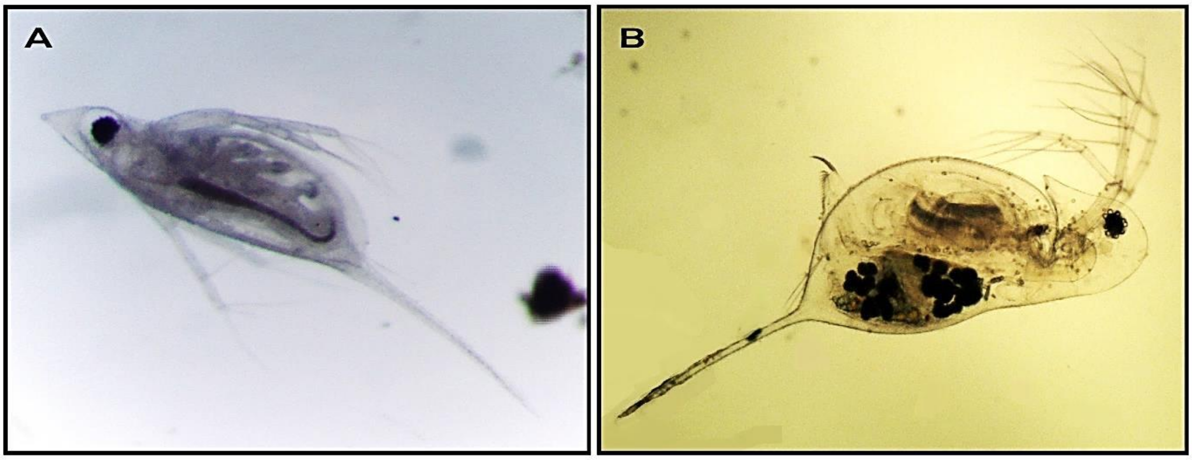


Figure 3.6: Micrographs depicting differences in tail spine length and helmet size of *Daphnia laevis* Birge, 1879 sampled in two consecutive years from the Okavango Delta, Botswana. **A**: *D. laevis* sampled from the Okavango Panhandle in August 2011. **B**: *D. laevis* sampled from the flooded Thaoge Channel, Okavango Delta Fan in August 2012.

REPRODUCTION

Cladoceran reproduction is similar to that of the majority of rotifers in that it is mostly parthenogenetic or asexual, but sexual reproduction takes place during times of stress (Seaman *et al*. 1999; Forró *et al.* 2008). Subitaneous eggs without a resting stage develop in the brood chamber (Figs. 3.7A & 3.7B) before juveniles, which resemble the mother, are released into the surrounding environment (Figs. 3.7C – F). The young female individuals may produce eggs in their own brood pouches within two to three days after their birth (Seaman *et al*. 1999).

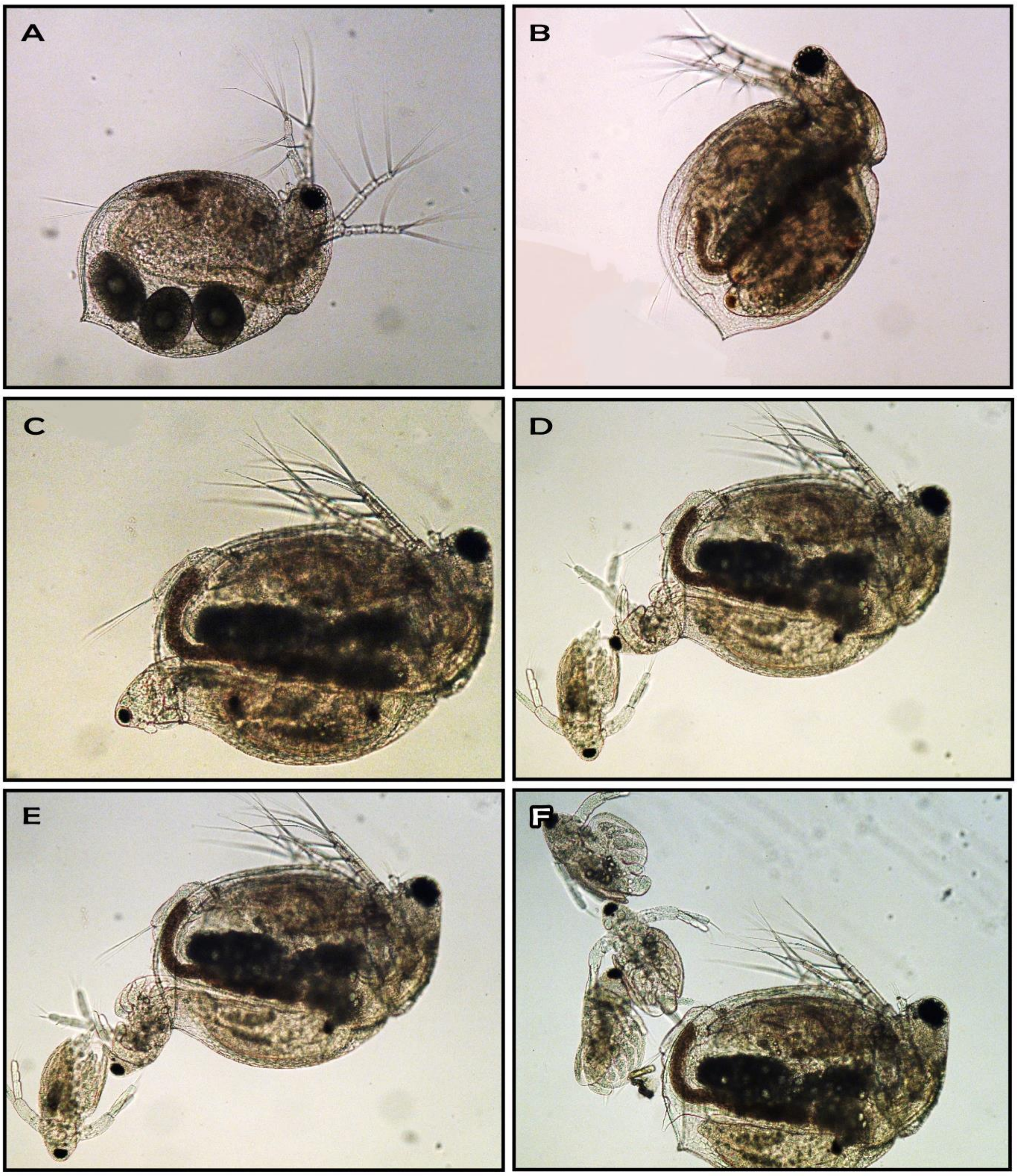


Figure 3.7: Micrographs of female *Ceriodaphnia reticulata* (Jurine, 1820) individuals reproducing by means of parthenogenesis. The population was sampled from a pool at the village of Mohembo, Okavango Panhandle, in August 2012. **A**: A female individual with subitaneous eggs in her brood chamber. **B**: A female individual with juvenile clones of herself in her brood chamber. **C** – **F**: A female individual releasing young female offspring into the surrounding environment.

When conditions are unfavourable, male offspring are produced, resulting in mating and the formation of fertilised resting eggs. These eggs are encased by a hard, resistant shell which, in a number of families, is protected by the moulted carapace of the mother. This protective shell is known as the ephippium. Some ephippia sink to the bottom of the water body, while others float to the surface and may be found in large numbers along the shoreline (Seaman *et al*. 1999). These sexually produced diapausing eggs are important propagules for passive dispersal. They are able to resist desiccation and other unfavourable conditions, including surviving passage through the digestive tract of birds (Forró *et al.* 2008).

Due to the fact that clones are produced, two or more populations of the same species, but which differ genetically, may occur in the same or adjacent water bodies. The timespan between sexual reproduction determines the extent and effect cloning has on genetic diversity. Sexual reproduction, however, has not yet been recorded in all populations (Seaman *et al*. 1999).

ECOLOGY

The majority of cladoceran species inhabit continental fresh or saline waters. Two ctenopods and a number of onychopods (family Podonidae) are true marine species. Furthermore, a few ctenopod, anomopod and onychopod species occur in brackish water, seven known species are true inhabitants of subterranean environments and a few chydorid species live in semi-terrestrial conditions (Forró *et al.* 2008).

Dole-Olivier *et al.* (2000) stated that it was previously assumed that cladoceran species were globally distributed, but that this is not the case. Only a number of species are reported to have a cosmopolitan distribution (Dole-Olivier *et al.* 2000). In order to define the global pattern of species distribution, a greater knowledge of their taxonomy is necessary as too many species are ‘vague’ compared to those that are ‘valid’ or ‘fair’ and their diversity is globally underestimated (Dole-Olivier *et al.* 2000; Korovchinsky 2006; Van Damme *et al*. 2013). Korovchinsky (2006) stated that some cladoceran taxa are absent from the tropics and the southern hemisphere. Species richness is concentrated in the warm, temperate, subtropical zone of both hemispheres and elevated areas of the true tropics. Some species have only been collected from a single water body, while others have extensive distribution ranges (Korovchinsky 2006).

Despite the general conclusion that endemism is low amongst the African Cladocera (Forró *et al.* 2008), recent studies indicate a significant endemism at the species and genus level (Van Damme *et al*. 2013). Southern Africa has a complex geological history and topography and the cladoceran fauna harbour a mixture of Afrotropical/Ethiopic, Palaearctic, circumtropical and local endemic elements. Hence, it can be expected that the Cladocera of the region have a high diversity and endemism.

Most members of the Cladocera are filter-feeders which consume algae, detritus and biofilms. They create a feeding current between the carapace lobes from which they collect fine suspended material. In some benthic species crawling and feeding are virtually part of the same mechanism. There are a few exceptions to the filter-feeders, which include scavengers and ectoparasites (Dole-Olivier *et al.* 2000).

Cladoceran populations are extremely influenced by temperature and are often seasonal. For example, *Daphnia* seem to be most common in spring, *Diaphanosoma excisum* is usually present during the summer heat and *Moina micrura* Kurz, 1874 is associated with turbid waters after rain storms (Seaman *et al*. 1999). Temperature has an influence on their life-cycle, abundance and distribution. Cold-water and thermophilic cladocerans do occur, but the majority of species are unable to survive temperatures above 30°C (Dole-Olivier *et al.* 2000).

CLADOCERA OF THE OKAVANGO AND ITS ASSOCIATED BASINS

Amongst all the groups of freshwater zooplankton, the majority of studies conducted in the Okavango region have focussed on the superorder Cladocera. These studies, however, remain only a handful and most do not include diversity. Studies on the Cladocera of the Okavango include that of Cronberg *et al*. (1995), Hart (1997), Høberg *et al.* (2002), Lindholm (2002), Hart *et al.* (2003), Hart & Dumont (2005), Lindholm *et al.* (2007; 2009), Lindholm & Hessen (2007), Siziba *et al*. (2011a; 2011b; 2013). The results of these studies are summarised, discussed and compared to that of the present study in **Chapter 6**. No data is available for the Cladocera of Lake Ngami, the Boteti River, Lake Xau or the Nata River.

COPEPODA

Copepods most likely diverged from other arthropod taxa between 522 and 388 million years ago and outnumber all other multicellular animal groups, including nematodes and insects. They are an extremely diverse group with respect to physiology, morphology, life-strategy and habitat preference and inhabit the majority of natural and man-made aquatic systems, from nutrient-rich oceans to the nutrient-poor waters of the highest mountain lakes. There are also those species which have left the traditional aquatic habitats in exchange for leaf litter, sand grains and rain forest canopies. Others have evolved to colonise hot springs, hyper-saline waters and caves, as well as to form symbiotic associations with other species of plants and animals (Hairston & Bohonak 1998; Bron *et al.* 2011; Boxshall & Defaye 2008). Copepods originated in the marine environment where the greatest diversity is found, but approximately 2,814 species have colonised almost all freshwater habitats (Boxshall & Defaye 2008).

Copepods form critical components of the world's aquatic ecosystems and are cornerstones in aquatic food webs. These secondary producers consume micro-organisms and serve as primary prey for early life history stages of many economically important fish, amongst others (Bron *et al.* 2011). Bron *et al.* (2011) stated that this group of crustaceans contribute considerably to ecosystem services, both marine and freshwater, with an estimated value of 22.6 trillion USD per year.

CLASSIFICATION AND SYSTEMATICS

Five orders of the subclass Copepoda inhabit freshwater (Table 3.3) and have adopted a range of life styles including particle-feeding, predation and parasitism (Boxshall & Defaye 2008). Only three of these orders inhabit freshwater ecosystems in southern Africa, namely the Calanoida (Fig. 3.8A), Harpacticoida (Fig. 3.8B) and Cyclopoida (Fig. 3.8C) (Table 3.3) (Rayner 2001).

Table 3.3: Freshwater copepod orders and families as well as number of genera and species currently known in the Afrotropical geographic area and worldwide. Numbers in parentheses = endemic species. Summarised from Boxshall & Defaye (2008).

Taxa	**Afrotropical**		**World**	
	Genera	**Species**	**Genera**	**Species**
Order Calanoida	7(3)	72	73(45)	552
Family Diaptomidae	7(3)	72	60(40)	441
Family Centropagidae	0	0	8(5)	79
Family Temoridae	0	0	4(0)	30
Family Aetideidae (*Senecella*)	0	0	1(0)	2
Order Harpacticida	15(1)	108	76(36)	1124
Family Canthocamptidae	6(1)	46	38(21)	627
Family Parastenocarididae	1(0)	34	6(4)	249
Family Ameiridae	3(0)	9	9(4)	149
Family Miraciidae (Diosaccidae)	1(0)	13	2(1)	53
Family Ectinosomatidae	0	0	6(2)	13
Family Phyllognathopodidae	1(0)	3	3(2)	10
Family Harpacticidae	0	0	1(1)	4
Family Chappuisiidae	0	0	1(1)	2
Family Huntemanniidae	1(0)	1	2(0)	6
Family Laophontidae	2(0)	2	6(0)	7
Family Cletodidae	0	0	1(0)	3
Family Darcythompsoniidae	0	0	1(0)	1
Order Cyclopoida	38(6)	225	98(52)	1096
Family Cyclopidae	25(2)	167	55(24)	800
Family Oithonidae	0	0	2(0)	7
Family Ozmanidae	0	0	1(1)	2
Family Lernaeidae	7(3)	39	16(11)	114
Family Ergasilidae	6(1)	19	24(16)	173

Table 3.3 (continued): Freshwater copepod orders and families as well as number of genera and species currently known in the Afrotropical geographic area and worldwide. Numbers in parentheses = endemic species. Summarised from Boxshall & Defaye (2008).

Taxa	**Afrotropical**		**World**	
	Genera	**Species**	**Genera**	**Species**
Order Gelyelloida	0	0	1(1)	2
Family Gelyellidae	0	0	1(1)	2
Order Siphonostomatoida	0	0	9(4)	40
Family Lernaeopodidae	0	0	7(4)	38
Family Caligidae	0	0	1(0)	1
Family Dichelesthiidae	0	0	1(0)	1
Total	60(10)	405	257(138)	2814

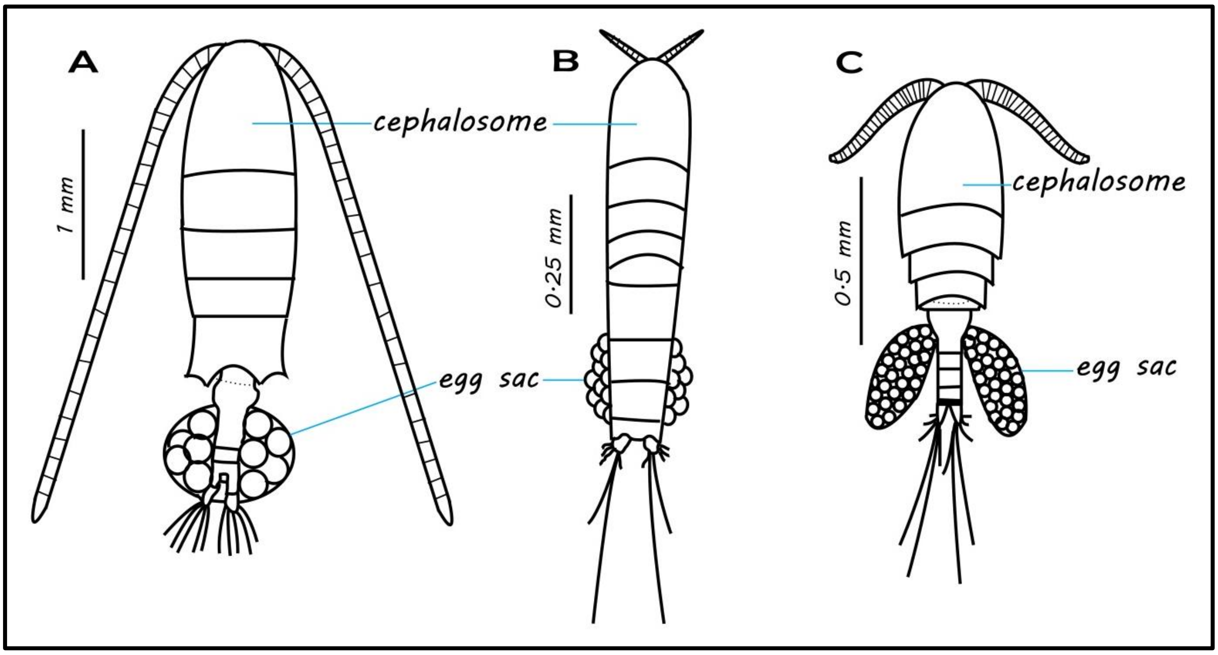


Figure 3.8: Diagram of the dorsal view of free-living, freshwater, female Copepoda. **A**: Calanoida. **B**: Harpacticoida. **C:** Cyclopoida (Redrawn from Rayner 2001).

Following the major contributions of Sars (1927) and Kiefer (1934), no taxonomic research was conducted on the free-living, freshwater Copepoda of southern Africa until 1981. More recently a number of studies were conducted on the Calanoida in southern Africa, which included, amongst others, a revision of the *Lovenula* Schmeil, 1898 (Rayner 1992) and the description of distribution patterns (Hart & Rayner 1994; Rayner & Heeg 1994) and a number of new species (Rayner 1994; Rayner 1999a). No taxonomic research has been conducted on the order Cyclopoida and Harpacticoida from southern Africa post 1934 (Rayner 2001).

Members of the order Harpacticoida are excluded from the plankton as they inhabit the benthos of lentic and lotic habitats (Dole-Olivier *et al.* 2000) and amongst the order Cyclopoida only three families are found in southern African continental waters. Amongst these, two families (Lernaeidae and Ergasilidae) are parasitic for at least part of their life-cycle (Boxshall & Defaye 2008), while Cyclopidae is the only cyclopoid family with free-living freshwater representatives in southern Africa. Members of the order Calanoida on the subcontinent are represented by individuals of the family Diaptomidae only. Hence, planktonic, freshwater, free-living copepods of southern Africa are comprised of two families, namely Diaptomidae (Calanoida) and Cyclopidae (Cyclopoida) which will be discussed in more detail.

CALANOIDA

The six families of calanoid copepods include species from freshwater systems, coastal lakes and estuaries as well as relict marine species (Rayner 1999b). Dussart (1980) recorded calanoid species from three families (Acartiidae, Pseudodiaptomidae and Diaptomidae) on the African continent. The Acartiidae and Pseudodiaptomidae are found in coastal lakes and estuaries only (Rayner 1999b).

Diaptomidae

The Diaptomidae comprises about 440 (primarily freshwater) species in four subfamilies. The two largest of these subfamilies, the Diaptominae and Paradiaptominae, comprise 410 and 24 species, respectively (Boxshall & Defaye 2008). In the inland waters of Africa, all calanoid copepods belong to the Paradiaptominae or Diaptominae (Rayner 2001).

Paradiaptominae

The genera *Metadiaptomus* Methuen, 1910*, Lovenula, Neolovenula* Gauthier, 1938 and *Paradiaptomus* Sars, 1895 belong to the subfamily Paradiaptominae (Rayner 1999b). Apart from a few exceptions, they are restricted to Africa (Rayner 2001; Boxshall & Defaye 2008). There is no fossil evidence to relate freshwater copepods in Africa to any particular geological period, but the distribution of Paradiaptominae (Africa, Madagascar, Mediterranean, India and Sri Lanka) suggests that this group may be Gondwanian in origin. All species of the subfamily Paradiaptominae were described more than 60 years ago, with the exception of three new species of the genus *Paradiaptomus* described by Rayner (1999a) 17 years ago. There has been much confusion in Paradiaptominae taxonomy as their characters are very clearly defined, with the smallest variability in morphology almost certainly indicating a different species. This has caused misidentifications and errors (Rayner 1999b).

Diaptominae

Unlike the subfamily Paradiaptominae, the more than 40 genera belonging to the subfamily Diaptominae mainly have a worldwide distribution (Boxshall & Defaye 2008) with only two (*Tropodiaptomus* Kiefer, 1932 and *Thermodiaptomus* Kiefer, 1932) occurring in sub-Saharan Africa and one (*Thermodiaptomus*) being endemic to the continent (Hart & Rayner 1994; Rayner 1999b). There are a large number of species in this subfamily of calanoid copepods and they seem to be speciating fast, especially the tropodiaptomids (Rayner 1999b).

CYCLOPOIDA

Cyclopidae

The most abundant and successful of the freshwater Copepoda are the Cyclopoida. In inland waters, the Cyclopidae is represented by more or less 35 genera and 590 known species (Hairston & Bohonak 1998). Some of the southern African, free-living cyclopoid species (Family Cyclopidae) have a worldwide distribution. Genera which have been collected from the inland waters of southern Africa include *Acanthocyclops* Kiefer, 1927, *Ectocyclops* Brady, 1904, *Eucyclops* Kiefer, 1927, *Macrocyclops* Claus, 1893, *Mesocyclops* Sars, 1914, *Metacyclops* Kiefer, 1927, *Microcyclops* Claus, 1893, *Paracyclops* Claus, 1893, *Thermocyclops* Kiefer, 1927 and *Tropocyclops* Kiefer, 1927, but some authors consider these genera to be subgenera of *Cyclops* Müller, 1785 (Rayner 2001). Information on the southern African cyclopoids and harpacticoids remains limited. Most species were described between 1904 and 1934 by taxonomists such as G. Stewardson Brady, Georg Osian Sars and Frederick Kiefer (Reid *et al*. 2000; Rayner 2001).

MORPHOLOGY

The total length of an adult copepod excludes the furcal setae (Fig. 3.9) and in freshwater free-living forms this ranges from 0.2 to 5.0 mm (Dole-Olivier *et al.* 2000). The body somites refer to body divisions or segments, which, together with appendages of free-living, freshwater Copepoda, are indicated in Figures 3.9A and 3.9B. In all adult copepods the maxilliped-bearing first thoracic somite is incorporated in the cephalosome. The first pedigerous somite is the second thoracic somite which may or may not be incorporated in the cephalosome (Fig. 3.9A). The dorsal side of the cephalosome is covered by a cephalic shield. Five pairs of appendages are present on the cephalon, namely: antennules (A1), antennae (A2), mandibles (Md), maxillules (Mx1) and maxillae (Mx2). The first thoracic somite carries a pair of maxillipeds (Mxp) (Dole-Olivier *et al.* 2000; Rayner 2001).

The rest of the thorax, known as the metasome, consists of five pedigerous somites (Pdg 1-5). In calanoids the fourth and fifth pedigerous somites may be fused. The first four somites (Pdg 1-4) each possesses a pair of swimming legs (natatory legs), while the legs on the fifth somite (Pdg 5) are not used for swimming (non-natatory) in cyclopoids and most calanoids. A hinged articulation which divides the body into the prosome and urosome is present between the fifth pedigerous somite and the genital somite (GS) (gymnoplean condition) in calanoids and between the fourth and fifth pedigerous somites (podoplean condition) in cyclopoids (Rayner 2001).

The urosome consists of two or three somites in female calanoids, five somites in male calanoids and five somites in female and male cyclopoids. It has no appendages in calanoids, but a vestige of the fifth leg pair in cyclopoids; it terminates in paired furcae which are attached to the anus-bearing anal somite (AS). The furcal ramus of calanoids bears five setae and a sixth dorsal seta, while that of cyclopoids have many long setae. Other diagnostic characteristics may include, but are not limited to, spines, spinules, setae, setules, armour, claws, egg sacs and pigmentation (Dole-Olivier *et al.* 2000; Rayner 2001).

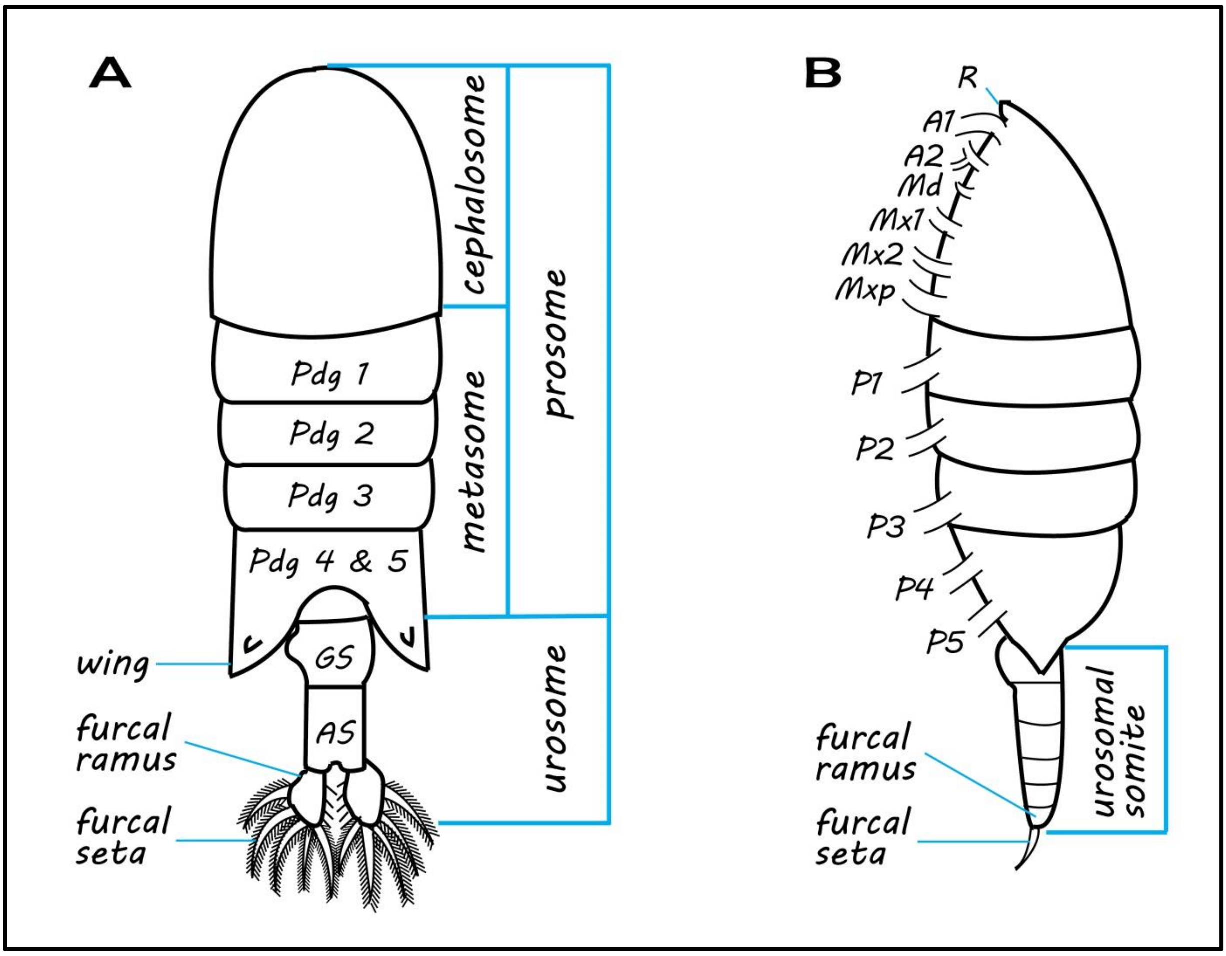


Figure 3.9: Diagram of free-living, freshwater Calanoida indicating details of somites and appendages. **A**: Female in dorsal view. **B**: Male in lateral view (Redrawn from Rayner 2001). KEY: Pdg 1-5 = pedigerous somites 1-5; GS = genital somite; AS = anal somite; R=rostrum; A1 = antennule; A2 = antenna; Md = mandible; Mx1 = maxillule; Mx2 = maxilla; Mxp = maxilliped; P1-P4 = swimming legs; P5 = modified, non-swimming leg.

MALE MORPHOLOGY

Copepod males and females differ distinctly in size, so much so that in certain calanoid species males may be half the length of females. Male members of the order Calanoida have more urosomal somites than females and they display other morphological differences in appendages such as the fifth pair of legs and the antennules. The right antennule is geniculate or hinged (Fig. 3.10A). In cyclopoids, the male's antennules are bilaterally geniculate (Fig. 3.10B) (Rayner 2001).

REPRODUCTION

Sexual reproduction is the rule amongst all free-living, freshwater Calanoida and Cyclopoida. They use their modified appendages and antennules to capture females (Fig. 3.10C) and fertilisation takes place when a male attaches a spermatophore to a female copulatory pore (Fig. 3.10D). Pre-copulatory mate guarding is common among cyclopoids and after copulation, females store sperm in subcuticular spermathecal sacs known as 'receptaculum seminis'. Thereafter, eggs are fertilised and extruded into egg sacs. (Dole-Olivier *et al.* 2000; Rayner 2001). The order Calanoida produces a single egg sac (Fig. 3.10E) in which eggs are carried on the ventral side of the female urosome, while cyclopoids have a pair of egg sacs (Fig. 3.10F) (Rayner 2001). The development times of eggs correlate strongly with temperature (Rayner 2001) and brood size varies from 100 to one or two eggs (Dole-Olivier *et al.* 2000).

Copepods have a multipart life-history, composed of different instars. Primitively, the life-cycle of free-living copepods includes six naupliar stages and six copepodid stages, the last of which (C6) is the adult (Hairston & Bohonak 1998; Dole-Olivier *et al.* 2000; Rayner 2001). The most dramatic alteration in morphology, such as changes in segmentation, body size and appendage structure, takes place during the transition from the sixth naupliar stage to the first copepodid stage (Hairston & Bohonak 1998; Dole-Olivier *et al.* 2000).

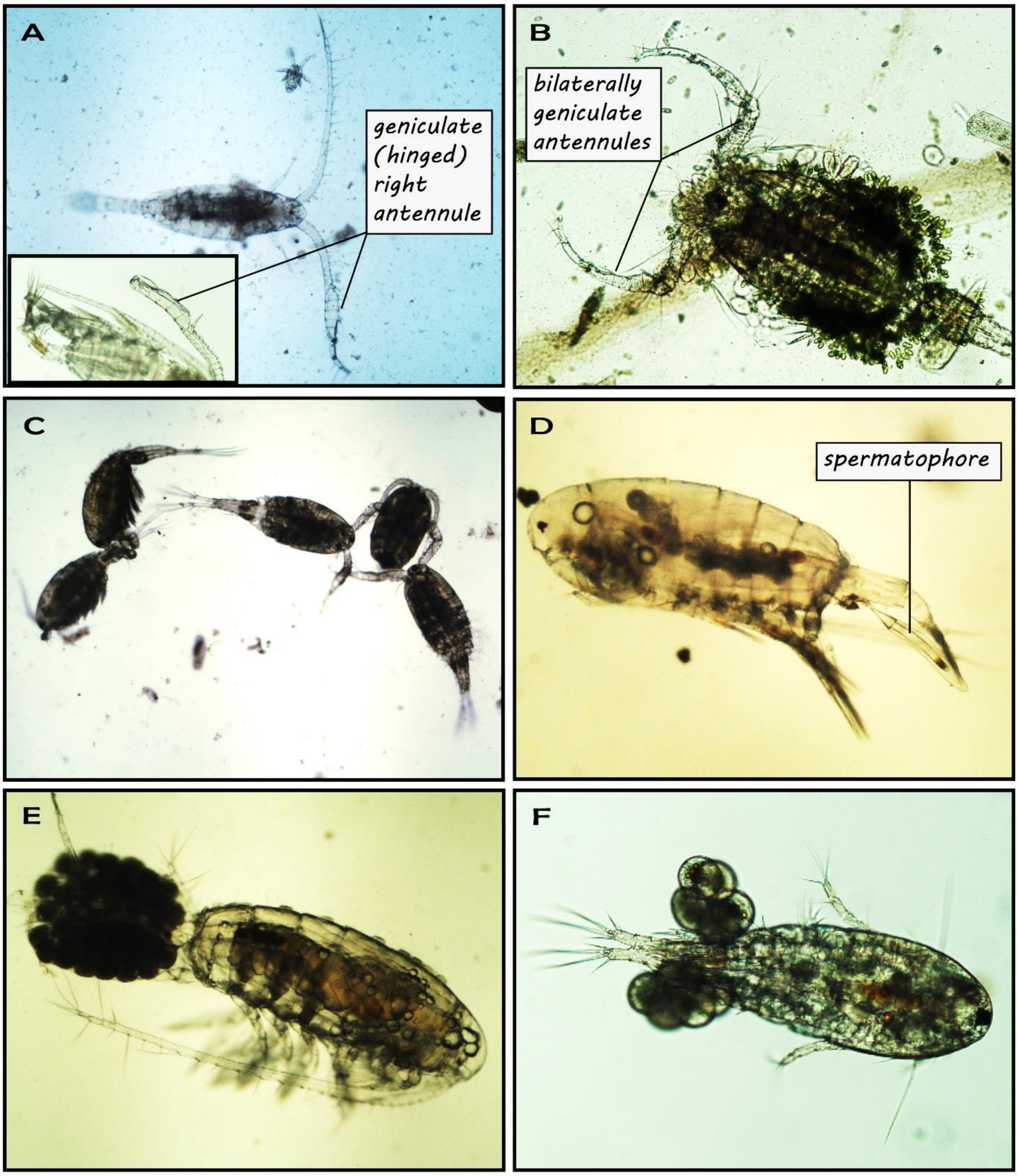


Figure 3.10: Light micrographs of Copepoda sampled from water bodies in northern Botswana in August 2012 and 2013. **A**: Male Calanoida with a geniculate or hinged right antennule. **B**: Male Cyclopoida (covered in sessile ciliate symbionts) with bilaterally geniculate antennules. **C**: Male Cyclopoida using their modified appendages and antennules to capture females for fertilisation. **D**: Female Calanoida with a spermatophore attached to the copulatory pore on the genital somite (GS). **E**: Female Calanoida with a single egg sac. **F**: Female Cyclopoida with a pair of egg sacs.

DIAPAUSE

All environments temporarily vary and may at times limit growth, reproduction or survival. This is especially true in ephemeral water bodies which dry up from time to time. Copepods can avoid or survive harsh periods by entering diapause either in the form of resting eggs or dormant copepodid stages (Hairston & Bohonak 1998; Rayner 2001). It is known that members of the family Cyclopidae diapause as copepodids (Hairston & Bohonak 1998). Interestingly, fertilised, adult, female cyclopoids in a diapausing state have been recorded from a Norwegian Lake. Unfortunately, no information is available on the diapausing stages of the orders Calanoida and Cyclopoida of Sub-Saharan Africa (Rayner 2001).

Egg densities in the “egg banks” of both continental and marine aquatic environments range between 10^4 and 10^6 m^{-2} and maximum and mean age ranges are between two and 300 years and one and 70 years, respectively. The hatching of a variable portion of diapausing eggs, therefore, is delayed, depending on the species or habitat or both. It has been suggested that diapause “pre-adapted” the Copepoda for invading inland waters (Hairston & Bohonak 1998). Hairston & Bohonak (1998) argued a very valid point in that the pattern of success and diversification in families which have diapause is so clear that it is extremely important to look carefully for some form of diapause in all continental (freshwater) taxa and not just to conclude that they do not possess the trait (see **Chapter 8**).

ECOLOGY

In southern Africa, free-living freshwater copepods occupy a variety of habitats, including large impoundments, temporary water bodies, backwaters of rivers, marshes, vleis (shallow, marshy, natural pools of water which are mostly inundated seasonally) and coastal lakes, but do not occur in the main flow of rivers. Although a few species have colonised man-made lakes (Rayner 2001), members of the subfamily Paradiaptominae are generally adapted to extreme habitats such as arid environments and temporary water bodies (Rayner 2001; Boxshall & Defaye 2008). Tropodiaptomid and thermodiaptomid species colonise more permanent waters and occur in the warm, subtropical regions of northern Botswana and Namibia as well as in Mpumalanga and KwaZulu Natal in South Africa. In general, the majority of freshwater calanoids have very specific habitat preferences and a number of species are found within narrow geographical limits only (Rayner 2001).

As previously mentioned, members of the order Cyclopoida are the most successful and diverse group of freshwater copepods and some of the species which occur in southern Africa have a global distribution (Rayner 2001). The family Cyclopidae, in general, are cosmopolitan in freshwater (Boxshall & Defaye 2008). They occur in basically any type of aquatic habitat, including, but not limited to lakes, ponds, temporary pools, wells, streams and river floodplains (Rayner 2001).

Calanoids of the genus *Lovenula* are predators and capture prey using their large raptorial maxillipeds. Species of the genus *Paradiaptomus* have less-developed raptorial maxillipeds than those of the genus *Lovenula*. Most calanoids, however, are herbivorous and feed on phytoplankton and other fine particles (Rayner 2001). The majority of cyclopoids are predators that seize and tear prey such as rotifers, oligochaetes, chironomid larvae, small cladocerans, cladoceran juveniles and even copepod copepodites and nauplii (Dole-Olivier *et* al. 2000; Rayner 2001). On the other side, copepods are preyed on by other invertebrates such as water mites and Odonata nymphs as well as by juvenile fish (Rayner 2001).

Copepod species compositions are determined, amongst others, by pH and circumneutral conditions are most favourable, although some copepods are adapted to a wide range of pH. Temperature also has an influence on their abundance and distribution as it influences their life-cycle. The latitudinal and altitudinal range of species may be limited by temperature (Dole-Olivier *et* al. 2000).

COPEPODA OF THE OKAVANGO AND ITS ASSOCIATED BASINS

Members of the subclass Copepoda are the least studied group of zooplankton in the Okavango and its associated basins. Studies include Hart (1997), Hart *et al.* (2003), Lindholm & Hessen (2007), Siziba *et al*. (2011a; 2011b; 2013). These results are summarised, discussed and compared to that of the present study in **Chapter 7**. Data is not available for the Copepoda species diversity of Lake Ngami, the Boteti

River, Lake Xau and the Nata River as no copepod surveys have been conducted in these water bodies.

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*Not seen in original form

Chapter 4

MATERIALS AND METHODS

STUDY SITES

This study was carried out for a period of three years (2011 – 2013) during which time zooplankton was collected and water quality measured at a number of locations within each of the following water bodies in northern Botswana (Figs. 2.2 & 2.4):

- The Okavango Panhandle (Fig. 4.1)
- The outskirts of the Okavango Delta Fan (Fig. 4.2)
- The Thamalakane River, Maun (Fig. 4.2)
- Lake Ngami (Fig. 4.2)
- The Boteti River (Fig. 4.3)
- Lake Xau (Fig. 4.3), and
- The Nata River (see **Chapter 8**)

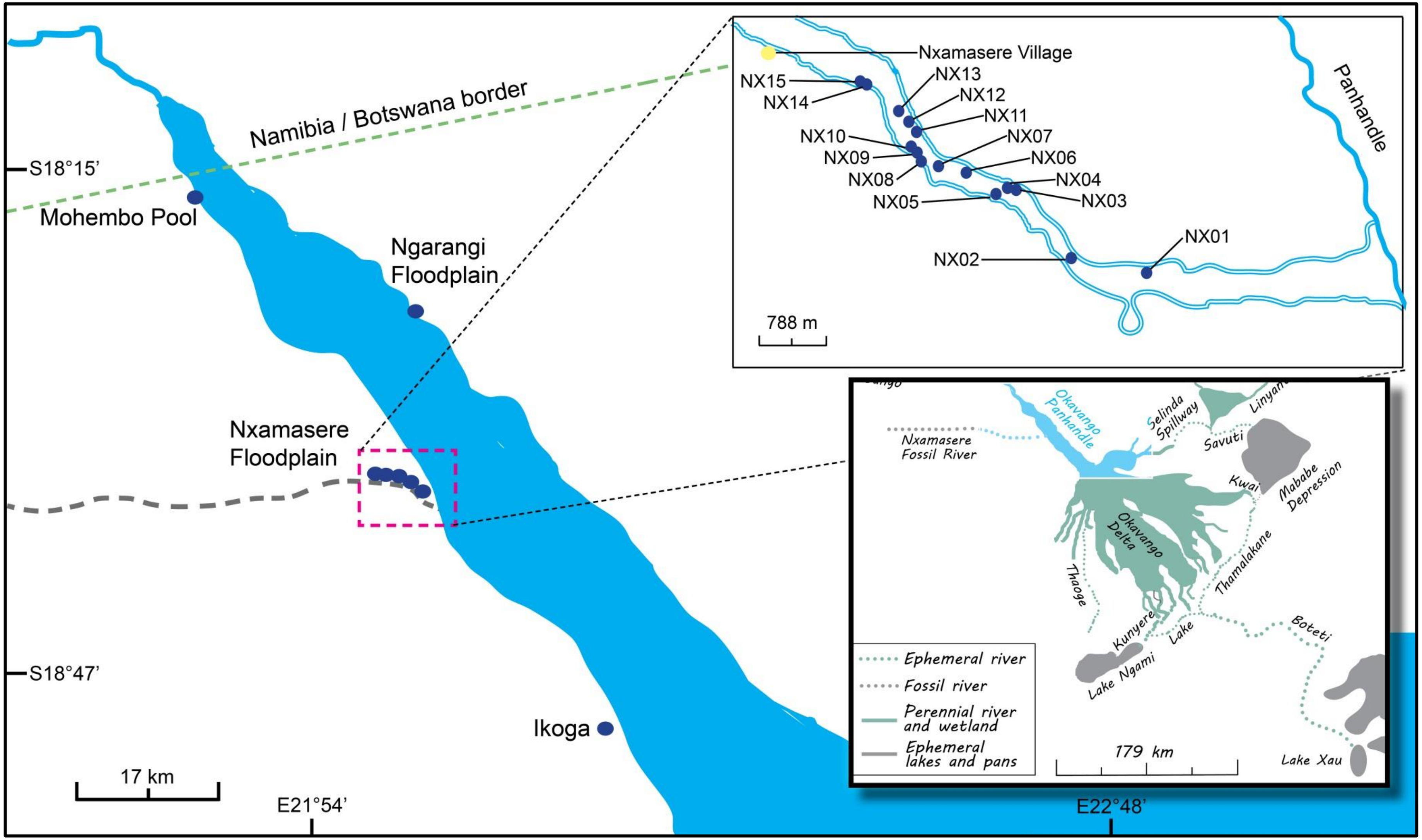

Figure 4.1: Map of the Okavango Panhandle indicating exact positions of sampling sites (blue dots) within the area, including Mohembo Pool, Ngarangi Floodplain, Nxamasere Floodplain samples 1 – 15 and Ikoga.

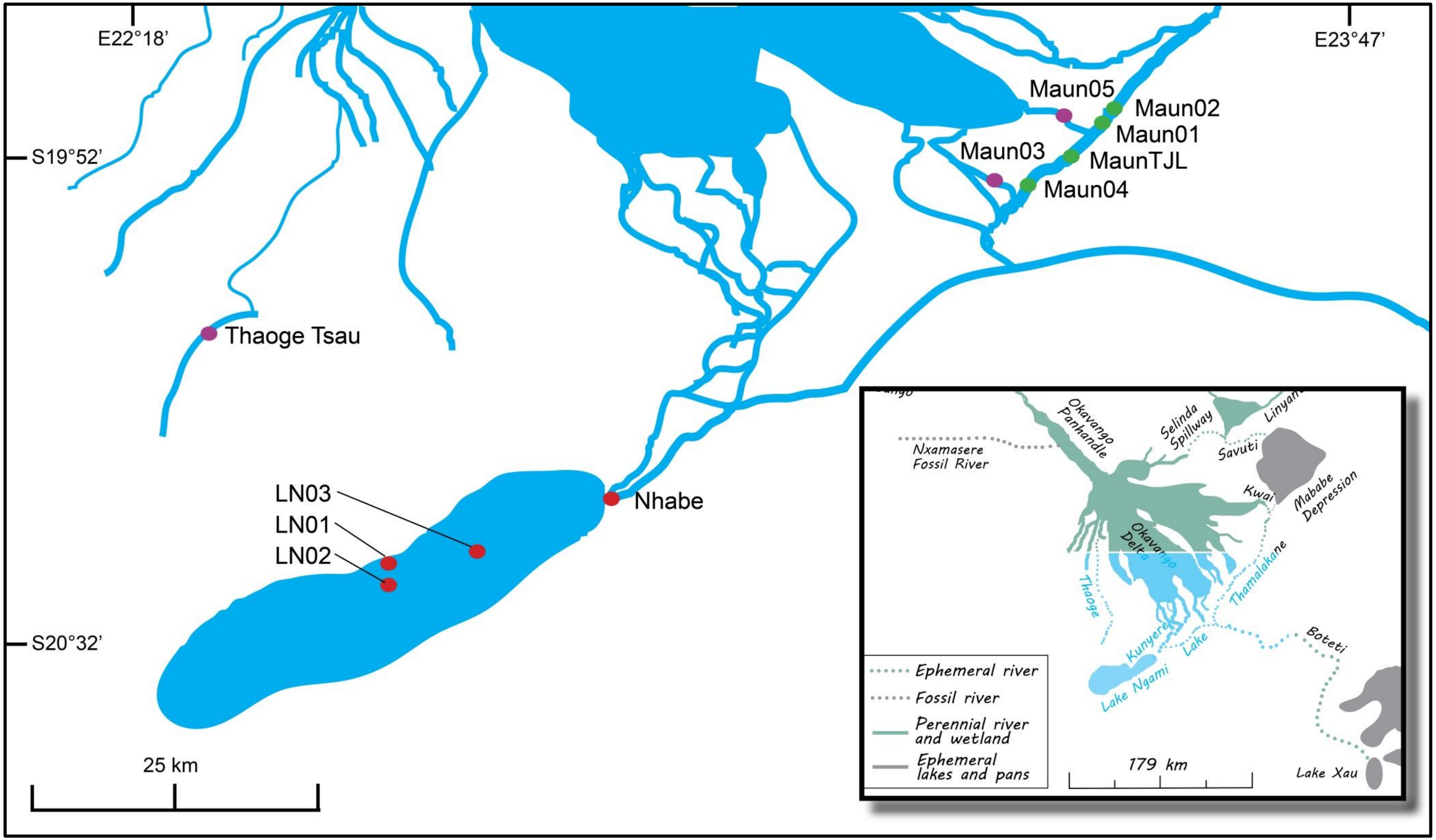

Figure 4.2: Map indicating the positions of sampling sites within the outer delta fan (purple dots), the Thamalakane River (green dots) and Lake Ngami (red dots), including Thaoge Tsau, Maun01 – Maun05, MaunTJL, Nhabe and LN01 - LN03.

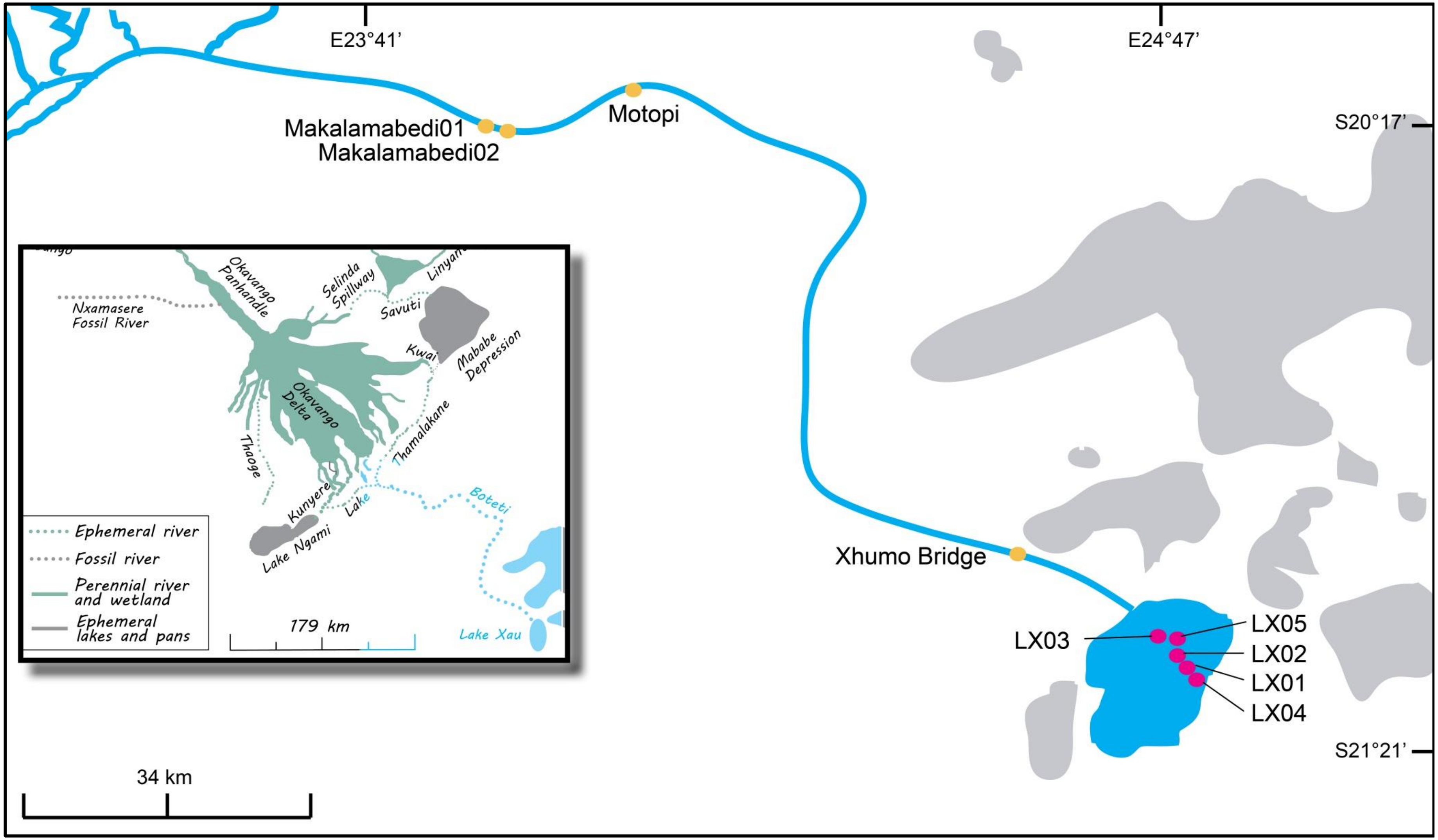

Figure 4.3: Map indicating the positions of sampling sites within the Boteti River (orange dots), and Lake Xau (pink dots), including Makalamabedi01 & 02, Motopi, Xhumo Bridge and LX01 - 05.

Study sites from the various water bodies (collectively referred to as the Okavango Delta and its associated basins) have been colour-coded for easy orientation as follows: Okavango Panhandle = blue; Okavango Delta = purple; Thamalakane River = green; Lake Ngami = red; Boteti River = orange and Lake Xau = pink (Tables 4.1 & 4.2).

Prior to any sample collection, site coordinates were determined and saved using a Garmin Colorado Geographical Positioning System (GPS) which will allow for sites to be revisited, if so required. All study locations and water bodies are indicated in Figs. 2.4, 4.1, 4.2 and 4.3 and a classification of the sampling sites by type of habitat is provided in Table 4.1. A list of the study sites and GPS coordinates is provided in Table 4.2. Study sites and GPS coordinates for the Nata River are provided in **Chapter 8**.

The Nata River originates in Zimbabwe and differs considerably to the Okavango Delta and its associated basins in terms of water chemistry, amongst others. It has, therefore, been dealt with as a separate unit in **Chapter 8** in the form of two scientific papers. The first paper has been prepared for submission to the *African Journal of Aquatic Science* and the second has been accepted for publication in *Acta Parasitologica* (West *et al*. in press).

Zooplankton was sampled during August 2011, August and September 2012 and July 2013. At this time (during all three years), the floods from Angola had passed the distal end of the delta and filled its associated basins (the Thamalakane River, Lake Ngami, the Boteti River and Lake Xau) to the south. The Nata River on the other hand had begun to dry, forming pools of various sizes in its lower reaches.

Table 4.1: Classification of sampling sites, sampled in July and August 2011, 2012 and 2013 in the Okavango Delta and its associated basins, by type of habitat.

Study site	**Type of habitat**	**Study site**	**Type of habitat**
Okavango Delta Panhandle		**Thamalakane River**	
Mohembo Pool	Pan connected to the Okavango River during high flow and disconnected during low flow.	Maun01	Flooded areas along the Thamalakane River.
Ngarangi Floodplain	Seasonally flooded swamp along the Ngarangi Side Channel.	Maun02	
NX01	Fossil river which is now a floodplain of the Okavango River. Water pushes up into the Nxamasere Fossil River during high flow and when the water recedes during the dry season pools of various sizes are left behind. These pools are rich in nutrients and contain high densities of aquatic plants.	Maun04	
NX02		MaunTJL	
NX03		**Lake Ngami**	
NX04		Nhabe	Riverine habitat.
NX05		LN01	Lake shore.
NX06		LN02	Centre of lake.
NX07		LN03	
NX08		**Boteti River**	
NX09		Makalamabedi01	Flooded areas along the ephemeral Boteti River.
NX10		Makalamabedi02	
NX11		Motopi	
NX12		Xhumo Bridge	
NX13		**Lake Xau**	
NX14		LX01	Shallow lake habitat which had been a dryland for a number of decades prior to inundation.
NX15		LX02	
Ikoga	A dryland area which only receives water during exceptionally high floods such as those of 2011 and 2012. No aquatic vegetation.	LX03	
Okavango Delta Fan		LX04	
Thaoge Tsau	Similar to 'Ikoga'.	LX05	
Maun03	Seasonally flooded floodplains.		
Maun05			

Table 4.2: Geographical Positioning System (GPS) coordinates for all study sites in the Okavango Delta and its associated basins, Botswana, sampled in July and August 2011, 2012 and 2013.

Study site	GPS coordinates	Study site	GPS coordinates
Okavango Delta Panhandle		**Thamalakane River**	
Mohembo Pool	S18 16.707 E21 47.287	Maun01	S19 55.664 E23 30.777
Ngarangi Floodplain	S18 24.815 E22 00.615	Maun02	S19 53.710 E23 32.102
NX01	S18 35.938 E22 01.694	Maun04	S20 00.281 E23 25.441
NX02	S18 35.844 E22 01.183	MaunTJL	S19 57.959 E23 27.911
NX03	S18 35.407 E22 00.772	**Lake Ngami**	
NX04	S18 35.391 E22 00.714	Nhabe	S20 24.527 E22 54.558
NX05	S18 35.122 E22 00.024	LN01	S20 28.980 E22 42.300
NX06	S18 35.286 E22 00.433	LN02	S20 30.143 E22 42.938
NX07	S18 35.260 E22 00.208	LN03	S20 27.647 E22 47.375
NX08	S18 35.224 E22 00.095	**Boteti River**	
NX09	S18 35.156 E22 00.070	Makalamabedi01	S20 19.483 E23 52.867
NX10	S18 35.122 E22 00.024	Makalamabedi02	S20 19.355 E23 55.092
NX11	S18 35.021 E22 00.057	Motopi	S20 12.799 E24 07.690
NX12	S18 34.953 E21 59.972	Xhumo Bridge	S21 07.190 E24 38.471
NX13	S18 34.865 E21 59.906	**Lake Xau**	
NX14	S18 34.698 E21 59.668	LX01	S21 16.958 E24 48.416
NX15	S18 34.679 E21 59.634	LX02	S21 16.437 E24 48.203
Ikoga	S18 50.515 E22 13.838	LX03	S21 16.184 E24 48.007
Okavango Delta Fan		LX04	S21 17.534 E24 48.613
Thaoge Tsau	S20 11.003 E22 28.121	LX05	S21 16.280 E24 48.208
Maun03	S20 01.859 E23 23.062		
Maun05	S19 55.356 E23 28.649		

FIELDWORK

FIELD LABORATORIES

In the Okavango Panhandle surveys were conducted from a base camp, namely the Leseding Research Camp. This camp was built by members of the Aquatic Ecology Research Group (Department of Zoology and Entomology, University of the Free State) and is situated on the premises of the Krokavango Crocodile Farm. Krokavango is located on the banks of Samochima Lagoon and on the fringes of

Samochima Village which lies on the western side of the Upper Panhandle close to Shakawe (Fig. 2.7). Leseding Camp is the perfect base from which to conduct research as it not only has neat tented accommodation (Fig. 4.4A), ablutions, and a sufficiently equipped kitchen (Fig. 4.4B), but also has a laboratory (Fig. 4.4C), aquarium (Figs. 4.4D & 4.4E) and two motor boats (Fig. 4.4F). Compound and dissection microscopes (Fig. 4.4C) as well as chemicals for the preservation of specimens, amongst others, were transported to Leseding from Bloemfontein.

When surveys were conducted in other areas, such as in and around Maun, Rakops and Nata Village, the necessary field and laboratory equipment was transported to these areas and temporary laboratories (very primitive at times) were set up wherever there was enough space at the lodges (Figs. 4.5A, 4.5B & 4.5C). Work was even carried out in bedrooms and on porches in extreme heat (Figs. 4.5D, 4.5E & 4.5F). A temporary laboratory was set up at the The Kraal in Maun (Fig. 4.5A) while sampling in the outskirts of the Okavango Delta Fan, the Thamalakane River and Lake Ngami. While sampling in the Boteti River and Lake Xau a laboratory was set up outdoors at a lodge on the outskirts of the village of Rakops (Figs. 4.5B, 4.5E & 4.5F), on the banks of the Boteti River. Here, electricity was only available at certain times of the day by means of a generator. The temporary field laboratory for sampling from the Nata River was set up in the bedroom of the author and a colleague at a lodge in Nata Village (Figs.4.5C & 4.5D).

ZOOPLANKTON COLLECTION, OBSERVATION AND PRESERVATION

Zooplankton was sampled from open waters and between aquatic vegetation by swooping a hand-held net, with a 50 µm pore aperture and a mouth diameter of 35 cm, vertically and horizontally through the water to cover different depths (Figs. 4.6A, 4.6B & 4.6C). Most floodplains, however, had a limited depth and zooplankton analysis was qualitative only. After collection, samples were transported to the temporary field laboratories where live observations were made using Nikon Eclipse E100 and Nikon SMZ800 light microscopes. For illustrations, photomicrographs were taken using a Nikon DS-Fi1 camera which can be attached to both the compound and dissecting microscopes (Figs. 4.4C, 4.5A, 4.5B & 4.5C). Samples were then halved and fixed in both 70% ethanol and 4% formaldehyde solutions (Figs. 4.5D, 4.5E & 4.5F) for long-term preservation and later identification of not only the zooplankton, but also their sessile ciliate symbionts. In the case of the mobiline ciliate, *Trichodina diaptomi* Šrámek-Hušek, 1953, infested calanoids were placed on slides and air-dried (see **Chapter 8**).

In 2011, samples were preserved with 70% ethanol and 4% formaldehyde solutions, respectively, immediately following collection, but back in the laboratory it was observed that a number of organisms detected in the field could no longer be found in the preserved samples. This was particularly true for many of the soft-bodied rotifers. The strategy of sampling, taking photomicrographs of live specimens and then fixing specimens was developed and followed in 2012 and 2013 and proved to be very successful in providing records of species present at the sampling sites. The general morphology of a number of rotifer taxa was distorted by fixatives and it is due to this that it was decided to omit the 2011 rotifer samples from this report. This study reports on members of the phylum Rotifera sampled from the study area in 2012 and 2013 and representatives of the superorder Cladocera and the subclass Copepoda sampled in 2011, 2012 and 2013.

WATER QUALITY MEASUREMENTS

In order to determine the environmental conditions at every sampling site, physical water quality parameters (visibility, temperature, dissolved oxygen concentration, conductivity, pH and salinity) were measured and biological observations were made (Figs. 4.6D, 4.6E & 4.6F). Water clarity was measured by making use of a Secchi disk (Fig. 4.6D), but the floodplains are mostly shallow and the water was clear, such that it was possible to see to the bottom. The remainder of the water quality parameters were determined using a Hanna HI 9828 Multiparameter (Figs. 4.6E & 4.6F), which was calibrated before departure from Bloemfontein and on a regular basis during surveys, according to the instructions by the manufacturer. This was a continuation of a previous study (West 2010; West *et al*. 2015). Water quality results measured during the present study are provided in Appendix 1, while that of the Nata River is presented in **Chapter 8**.

Figure 4.4: Leseding Research Camp close to Shakawe in the Upper Panhandle provides a perfect base from which to conduct research in the Okavango Panhandle, Botswana. **A**: Tented accommodation. **B**: Fully-equipped kitchen. **C**: Convenient laboratory. **D** & **E**: Aquarium. **F**: Two motorboats.

Figure 4.5: Temporary field laboratories were erected wherever possible in remote sampling areas in northern Botswana. **A**: Field laboratory at The Kraal, Maun. **B**: Outdoor laboratory in the vicinity of Rakops Village on the banks of the Boteti River. **C** & **D**: Temporary laboratory in the lodge room of two research group members in Nata Village. **E** & **F**: Temporary working sites for the quick preservation of specimens in the remote Rakops area.

Figure 4.6: Zooplankton and water quality samples were collected from the Okavango Delta and its associated basins in July and August 2011, 2012 and 2013. **A**: Zooplankton collection in the outskirts of the Okavango Delta, in and around Maun. **B**: Zooplankton collection in the Nxamasere Floodplain, Okavango Panhandle. **C**: Zooplankton collection in the crocodile ponds of Krokovango Crocodile Farm, Samochima Village. **D**: Visibility measurements with a Secchi disc in the Nxamasere Floodplain. **E**: Water quality measurements in the Nxamasere Channel, Okavango Panhandle. **F**: Water quality measurement in Lake Xau.

LABORATORY WORK

ZOOPLANKTON IDENTIFICATION

Once back in the laboratory in Bloemfontein, taxonomic classification of different microinvertebrate groups (Rotifera, Cladocera and Copepoda) was carried out using the following keys, amongst others:

- Athibai *et al.* (2013)
- Brain (2002)
- Dussart and Defaye (1995)
- Einsle (1971)
- Kiefer (1926)
- Kiefer (1929)
- Kořínek (1999)
- Methuen (1910)
- Nogrady *et al.* (1993)
- Orlova-Bienkowskaja (1998)
- Rayner (1999)
- Rayner (2001)
- Ricci and Melone (2000)
- Ruttner-Kolisko (1974)
- Sars (1916)
- Sars (1927)
- Scourfield and Harding (1966)
- Seaman *et al.* (1999)
- Segers (1995)
- Wallace and Snell (1991)

Identification was undertaken to the lowest possible taxonomic category, although taxonomically challenging groups, such as the family Chydoridae (Cladocera), were left in a higher taxonomic category. Identifications were confirmed by Dr. Nancy A. Rayner (University of the Free State, Bloemfontein, South Africa). In addition to the rotifers, cladocerans and copepods, ostracods were also sampled and preserved. Future, in-depth, taxonomic studies will be carried out on groups omitted from this document (Ostracoda), included as a species list only (Cyclopidae) or have been included as a higher taxonomic category (Chydoridae).

CILIATE SYMBIONT STAINING AND MORPHOLOGICAL MEASUREMENTS

The sessile ciliate symbionts, together with their zooplankton hosts, were placed in a 4% formaldehyde solution for long-term preservation and will be examined and identified for future publication. The air-dried smears of the mobiline ciliate, *Trichodina diaptomi*, were impregnated with silver nitrate using a modified version of Klein's technique, proposed by Lom (1958) and described by Wellborn (1967), in order to study details of the adhesive disc. See **Chapter 8** for a full description of the materials and methods used in this regard.

REFERENCE MATERIAL

All reference material of zooplankton and their symbionts has been allocated a reference number and deposited in the collection of the Aquatic Ecology Research Group of the Department of Zoology and Entomology, University of the Free State, South Africa.

ILLUSTRATIONS AND PHOTOGRAPHS

Photos and light micrographs are by the author and other members of the Aquatic Ecology Research Group, Department of Zoology and Entomology, University of the Free State, unless otherwise stated, in which case it has been provided by a particular group or individual for use in this document. All illustrations were prepared by the author.

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Chapter 5

TAXONOMIC ACCOUNT AND DISTRIBUTION OF ROTIFERA

INTRODUCTION

The rotifer record is highest in the Northern Hemisphere, most likely due to the lack of studies in the Southern Hemisphere. The African region, in particular, is the least studied (Segers 2008). In northern Botswana rotifer records include those conducted by Cronberg *et al.* (1995), Hart (1997), Green (2003) and Siziba *et al.* (2011). That of Green (2003) is the only comprehensive study with a specific focus on rotifers. Cronberg *et al.* (1995) conducted a hydrological study in the Kwando/Linyanti/Chobe System and included the presence of phytoplankton and zooplankton. Siziba *et al.* (2011) identified rotifers collected from a localised area south of Chief's Island (Fig. 2.7), while Hart (1997) compiled a limnological profile of the lower Okavango

Panhandle at Seronga (Fig. 2.7) based on 'a modest survey' conducted in 1986. Figure 5.1 indicates the areas in which these previous studies were conducted, as well as the rotifer sampling sites of the present study.

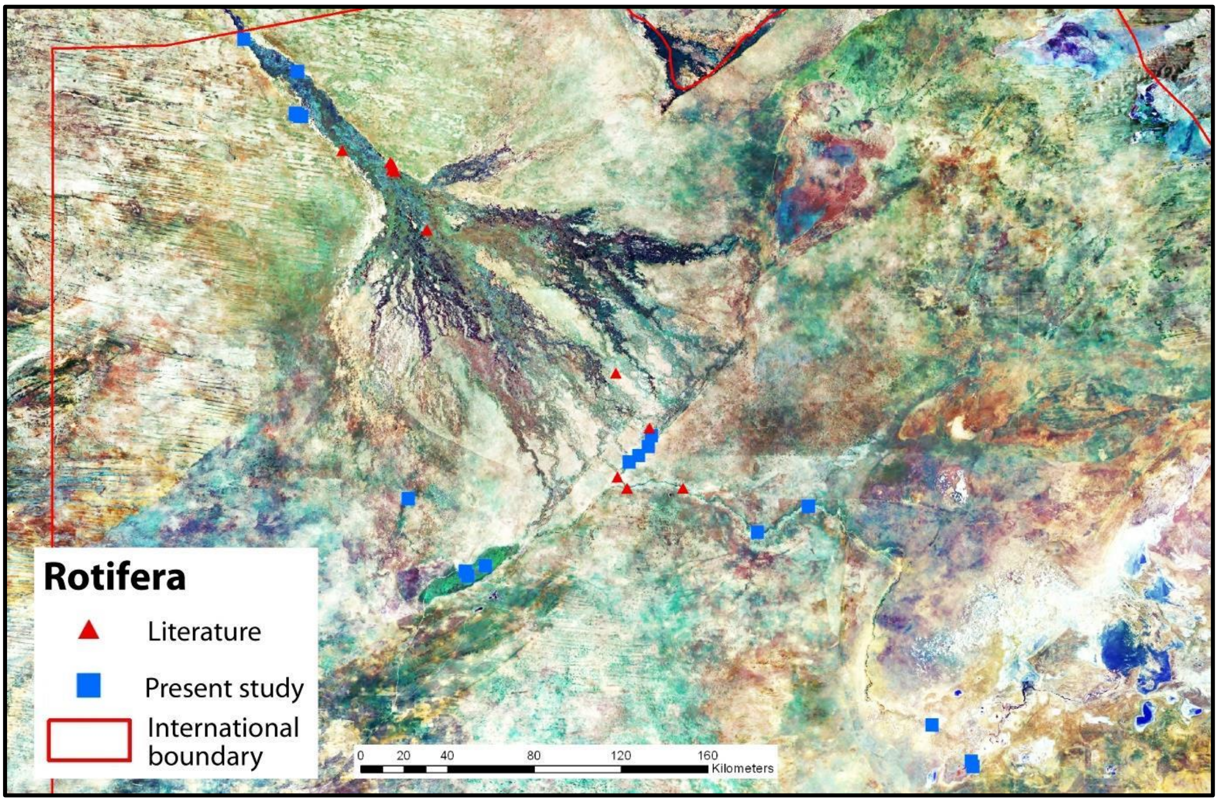

Figure 5.1: Geographic Information System (GIS) map indicating the sites within the Okavango Delta and its associated basins in northern Botswana where Rotifera samples were collected during the present study in 2012 and 2013 as well as where data was available for Rotifera from previous studies.

The aim of the present study was to determine the taxonomic composition of the phylum Rotifera from the Okavango Panhandle (which is completely neglected in terms of limnological research), parts of the Okavango Delta Fan as well as the ephemeral basins in northern Botswana which are associated with the Okavango Delta. No attempt has been made to study the systematics of Rotifera from the northern panhandle. Furthermore, the sampling of Rotifera from basins such as the lower Boteti River, Lake Ngami and Lake Xau have not been possible for 20 to 30 years due to continuing drought. The 2010 floods (see **Chapter 2**), however, provided a window of opportunity to sample from these systems which have already begun to dry again. This study also aimed at determining the distribution of rotifer species, amongst others, across the Okavanago Delta and its associated basins by combining data from previous studies with that of the present study. In this chapter the first ever records of Rotifera of the upper Okavango Panhandle, the Thaoge Channel (western Okavango Delta Fan) (Fig. 2.7), Lake Ngami, the lower Boteti River and Lake Xau (Figs. 2.4, 4.1, 4.2 & 4.3) are provided.

RESULTS AND REMARKS

Twenty four rotifer samples collected from 22 study sites in the Okavango Panhandle, Okavango Delta, Thamalakane River, Lake Ngami, Boteti River and Lake Xau revealed a total of 33 species which belong to 22 genera and 15 families (Table 5.1). These represented two orders (Ploima and Flosculariacea) under the class Monogononta as well as the order Bdelloidea under the class Digononta. All identified taxa are listed in Table 5.1.

The genus with the most representatives was *Brachionus* Pallas, 1766 (comprising six species), followed by *Trichocerca* Lamarck, 1801 (comprising three species). *Keratella* Bory de St. Vincent, 1822, *Lecane* Nitzsch, 1827, *Conochilus* Ehrenberg, 1834 and *Filinia* Bory de St. Vincent, 1824 were represented by two species each, while *Asplanchna* Gosse, 1850, *Asplanchnopus* de Guerne, 1888, *Anuraeopsis* Lauterborn, 1900, *Platyias* Harring, 1913, *Trichotria* Bory de St. Vincent, 1827, *Colurella* Bory de St. Vincent, 1824, *Epiphanes* Ehrenberg, 1832, *Euchlanis* Ehrenberg, 1832, *Monommata* Bartsch, 1870, *Scaridium* Ehrenberg, 1830, *Polyarthra* Ehrenberg, 1834, *Synchaeta* Ehrenberg, 1832, *Floscularia* Cuvier, 1798, *Sinantherina* Bory de St. Vincent, 1826, *Hexarthra* Schmarda, 1854, *Pompholyx* Gosse, 1951 and *Rotaria* Scopoli, 1777 all comprised a single species (Table 5.1).

Species diversity at the various study sites ranged from zero at Makalamabedi (a flooded area along the Boteti River) to 13 species at Maun04 (a floodplain of the Thamalakane River in the centre of Maun) and LN02 (in the centre of Lake Ngami).

Other study sites with a relatively high rotifer species diversity were LN01 along the shore of Lake Ngami (with 12 species), NX07 and NX03 in the Nxamasere Floodplain (with 11 and nine species, respectively), Xhumo Bridge, a floodplain in the lower reaches of the Boteti River (with 10 species), MaunTJL along the Thamalakane River (with nine species) and LX05 in Lake Xau (with nine species).

Species ranged from relatively widely distributed species to species which were only found at one or two study sites across the entire research area. The latter were usually low in numbers too. Species are listed from most diverse to least diverse in Table 5.2 and the study sites at which each was sampled are also provided. The most widely distributed species throughout the study area were species of the family Brachionidae, namely *Brachionus angularis* Gosse, 1851, *Keratella tropica* (Apstein, 1907), *Brachionus calyciflorus* Pallas, 1766 and *Keratella tecta* (Gosse, 1851). The least widely distributed species, such as *Trichocerca pusilla* (Jennings, 1903), *Floscularia ringens* (Linnaeus, 1758), *Hexarthra* sp., *Platyias quadricornis* (Ehrenberg, 1832), *Pompholyx sulcata* Hudson, 1885, *Rotaria neptunia* (Ehrenberg, 1830), *Sinantherina* sp. and *Synchaeta pectinata* Ehrenberg, 1832, were all only sampled at one sampling site, but in many cases this may be because they do not normally form part of the plankton and are benthic organisms.

Table 5.1: Monogonont and digonont rotifer taxa recorded in northern Botswana in 2012 and 2013.

PHYLUM ROTIFERA	
CLASS MONOGONONTA	
Order Ploima	
Family Asplanchnidae	**Family Epiphanidae**
Asplanchna brightwelli Gosse, 1850	*Epiphanes senta* (Müller, 1773)
Asplanchnopus multiceps (Schrank, 1793)	**Family Euchlanidae**
Family Brachionidae	*Euchlanis dilatata* Ehrenberg, 1832
Anuraeopsis fissa Gosse, 1851	**Family Lecanidae**
Brachionus angularis Gosse, 1851	*Lecane bulla* (Gosse, 1851)
Brachionus budapestinensis Daday, 1885	*Lecane papuana* (Murray, 1913)
Brachionus calyciflorus Pallas, 1766	**Family Notommatidae**
Brachionus caudatus Barrois & Daday, 1894	*Monommata grandis* Tessin, 1890
Brachionus falcatus Zacharias, 1898	**Family Synchaetidae**
Brachionus quadridentatus Herman, 1783	*Polyarthra remata* Skorikov, 1896
Keratella tecta (Gosse, 1851)	*Synchaeta pectinata* Ehrenberg, 1832
Keratella tropica (Apstein, 1907)	**Family Trichocercidae**
Platyias quadricornis (Ehrenberg, 1832)	*Trichocerca chattoni* (de Beauchamp, 1907)
Trichotria pocillum (Müller, 1776)	*Trichocerca elongata* (Gosse, 1886)
Family Colurellidae	*Trichocerca pusilla* (Jennings, 1903)
Colurella uncinata (Müller, 1773)	
Order Flosculariacea	
Family Conochilidae	**Family Flosculariidae**
Conochilus dossuarius Hudson, 1875	*Floscularia ringens* (Linnaeus, 1758)
Conochilus unicornis Rousselet, 1892	*Sinantherina* Bory de St. Vincent, 1826 sp.
Family Filiniidae	**Family Hexarthridae**
Filinia longiseta (Ehrenberg, 1834)	*Hexarthra* Schmarda, 1854 sp.
Filinia opoliensis (Zacharias, 1898)	**Family Testudinellidae**
	Pompholyx sulcata Hudson, 1885
CLASS DIGONONTA	
Order Bdelloidea	
Family Philodinidae	
Rotaria neptunia (Ehrenberg, 1830)	

Table 5.2: Distribution of Rotifera taxa collected in northern Botswana in 2012 and 2013. Taxa are presented from highest to lowest frequency. Study sites within the various water bodies are presented in a colour code as follows: 1. Okavango Panhandle, 2. Okavango Delta, 3. Thamalakane River, 4. Lake Ngami, 5. Boteti River and 6. Lake Xau. N indicates the number of water bodies in which the species were present.

ROTIFERA TAXA	STUDY SITES	N
Brachionus angularis Gosse, 1851	NX02, NX03, NX04, NX06, NX07, NX11, Taoge Tsau, Maun05, Maun04, MaunTJL, LN01, LN02, Xhumo Bridge, LX05. =14	6
Keratella tropica (Apstein, 1907)	NX02 NX03 NX04 NX06 NX07 NX11 MAUN05 Maun04, MaunTJL LN01, LN02, LN03 Xhumo Bridge, LX05. =14	6
Brachionus calyciflorus Pallas, 1766	NX03, NX07, MAUN03 Maun04, LN01, LN02, LN03 Xhumo Bridge, LX04 LX05. =10	6
Keratella tecta (Gosse, 1851)	NX02, NX06, MAUN03, MAUN05 Maun04, LN01, LN02, Motopi, LX04 LX05. =10	6
Lecane bulla (Gosse, 1851)	NX02, NX06, Taoge Tsau, Maun03, Maun04, MaunTJL, LN01, LN02, Xhumo Bridge. =9	5
Brachionus quadridentatus Herman, 1783	Maun03, Maun04, MaunTJL, LN01, LN02, Xhumo Bridge, LX05. =7	5
Asplanchna brightwelli Gosse, 1850	NX03, NX07, LN01, LN02, LN03, Xhumo Bridge, LX05. =7	4
Filinia longiseta (Ehrenberg, 1834)	NX07, NX11, MaunTJL, LN01, LN02, LX05. =6	4
Trichocerca chattoni (de Beauchamp, 1907)	NX04, Maun04, LN01, LN02, LX05. =5	4
Trichocerca elongata (Gosse, 1886)	NX03, Maun04, MaunTJL, LN01, LX05. =5	4
Brachionus caudatus Barrois & Daday, 1894	NX03, NX04, NX07, LN01, LN02, LN03, LX05.=7	3
Colurella uncinata (Müller, 1773)	Taoge Tsau, Maun03, Maun04, Xhumo Bridge. =4	3
Brachionus budapestinensis Daday, 1885	NX02, Maun04, LX04. =3	3
Conochilus dossuarius Hudson, 1875	NX03, Maun03, MaunTJL. =3	3
Euchlanis dilatata Ehrenberg, 1832	NX01, Maun04, Xhumo Bridge. =3	3
Lecane papuana (Murray, 1913)	NX02, LN01, Xhumo Bridge. =3	3
Polyarthra remata Skorikov, 1896	Mohembo Pool, NX06, NX07, NX11, LN02. =5	2
Brachionus falcatus Zacharias, 1898	Mohembo Pool, NX03, LN01, LN02. =4	2
Filinia opoliensis (Zacharias, 1898)	Mohembo Pool, NX03, MAUN05. =3	2
Anuraeopsis fissa Gosse, 1851	Maun04, LX04. =2	2

Table 5.2 (Cont.): Distribution of Rotifera taxa collected in northern Botswana in 2012 and 2013. Taxa are presented from highest to lowest frequency. Study sites within the various water bodies are presented in a colour code as follows: 1. Okavango Panhandle, 2. Okavango Delta, 3. Thamalakane River, 4. Lake Ngami, 5. Boteti River and 6. Lake Xau. N indicates the number of water bodies in which the species were present.

ROTIFERA TAXA	**STUDY SITES**	**N**
Asplanchnopus multiceps (Schrank, 1793)	Taoge Tsau, LX04. =2	2
Epiphanes senta (Müller, 1773)	Taoge Tsau, LN02. =2	2
Monommata grandis Tessin, 1890	NX07, Maun04. =2	2
Trichotria pocillum (Müller, 1776)	Taoge Tsau, MaunTJL. =2	2
Conochilus unicornis Rousselet, 1892	Ngarangi Floodplain, NX06, NX07. =3	1
Trichocerca pusilla (Jennings, 1903)	NX04, NX07. =2	1
Floscularia ringens (Linnaeus, 1758)	NX03. =1	1
Hexarthra Schmarda, 1854 sp.	NX03. =1	1
Platyias quadricornis (Ehrenberg, 1832)	MaunTJL. =1	1
Pompholyx sulcata Hudson, 1885	Maun03. =1	1
Rotaria neptunia (Ehrenberg, 1830)	Ngarangi Floodplain. =1	1
Sinantherina Bory de St. Vincent, 1826 sp.	NX07. =1	1
Synchaeta pectinata Ehrenberg, 1832	Xhumo Bridge. =1	1

ORDER PLOIMA

The order Ploima was the most dominant in the study area with representatives from nine families, 15 genera and 24 species (Table 5.1). In general it is the largest and most diverse group of monogononts, but does not include any colonial forms (Hochberg 2006).

FAMILY ASPLANCHNIDAE Eckstein, 1883

Members of the Asplanchnidae are commonly found in freshwater and are important predators amongst the rotifers, feeding on protozoans, other rotifers and micro-crustaceans, amongst others (Nandini & Sarma 2005). The Asplanchnidae were represented by two genera, namely *Asplanchna* and *Asplanchnopus*, in the present account (Table 5.1). Progressive adaptation to pelagic life has taken place within the Asplanchnidae. *Asplanchna* species have no foot (Fig. 5.2A), are fully adapted to floating and are entirely pelagic, while *Asplanchnopus* species have a reduced foot (Fig. 5.2B) to varying extents, are not as well adapted to floating and are semi-pelagic (Ruttner-Kolisko 1974). Representatives of *Asplanchnopus* are relatively rare in comparison to representatives of *Asplanchna* and information on the former is scarce. Since *Asplanchna* species are typically planktonic and *Asplanchnopus* species are littoral dwellers, it is unlikely that competition between the two genera is high under natural conditions (Nandini & Sarma 2005).

Genus *Asplanchna* Gosse, 1850 (Fig. 5.2A)

Under the genus *Asplanchna*, one species was identified and recorded during the present study, namely *Asplanchna brightwelli* Gosse, 1850 (Fig. 5.2A). *Asplanchna brightwelli* is large and often predatory (Gilbert 1968), feeding on representatives of smaller genera such as *Keratella* (Gilbert & Stemberger 1984). In the present study they were sampled from the Nxamasere Floodplain in the upper Okavango Panhandle, Lake Ngami, the lower Boteti River and Lake Xau (Table 5.2). Their presence and absence is strongly correlated with that of their prey species such as *Keratella tropica*. *Asplanchna brighwelli* has been sampled by a previous author (Green 2003) from the lower panhandle at Seronga, the lower delta, as well as in the upper reaches of the Boteti River (Fig. 5.2A).

Genus *Asplanchnopus* de Guerne, 1888 (Fig. 5.2B)

One single species of the genus *Asplanchnopus* was present in the study area, namely *Asplanchnopus multiceps* (Schrank, 1793). It is also the first record of the species and genus from the water bodies of northern Botswana.

Asplanchnopus multiceps is a predatory rotifer (Kotikova *et al.* 2004) and was sampled from two study sights, namely Thaoge Tsau, in the south-western portion of the Okavango Delta Fan (in the Thaoge Channel) (Fig. 4.2) and LX04 in Lake Xau (Fig. 4.3) in August 2012 (Fig. 5.2B). Both these study sites were inundated for the first time in decades. As mentioned previously (see **Chapter 2**), the Thaoge Channel began to dry in the 1850s and ceased to flow completely between 1877 and 1881 (Shaw 1983; 1985). The specific point along the Thaoge Channel where the sample was collected hasn't received water since the mid-70s ([1]Liversedge 2012, Personal communication). By the time Lake Xau received water in 2011, it had been completely dry since 1984 (Sallu *et al.* 2010).

It may be possible that *A. multiceps* was present due to recruitment from the egg banks. In other words, that it used to be present in the Okavango in the past, but that it has not been as successful in recent years. Hence, where water was present at relatively constant intervals no specimens were sampled, but in areas which have been dry for decades overwintering eggs lay dormant in the soil and once the water bodies were inundated, *A. multiceps* hatched from the egg banks. If these water bodies remained inundated for long enough it would be interesting to note whether *A. multiceps* would remain present or disappear and whether its disappearance is in fact due to competition by species such as *A. brightwelli* or due to other biotic or abiotic factors.

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[1] Dr. Tim Liversedge: Film-maker and environmentalist, Maun, Botswana.

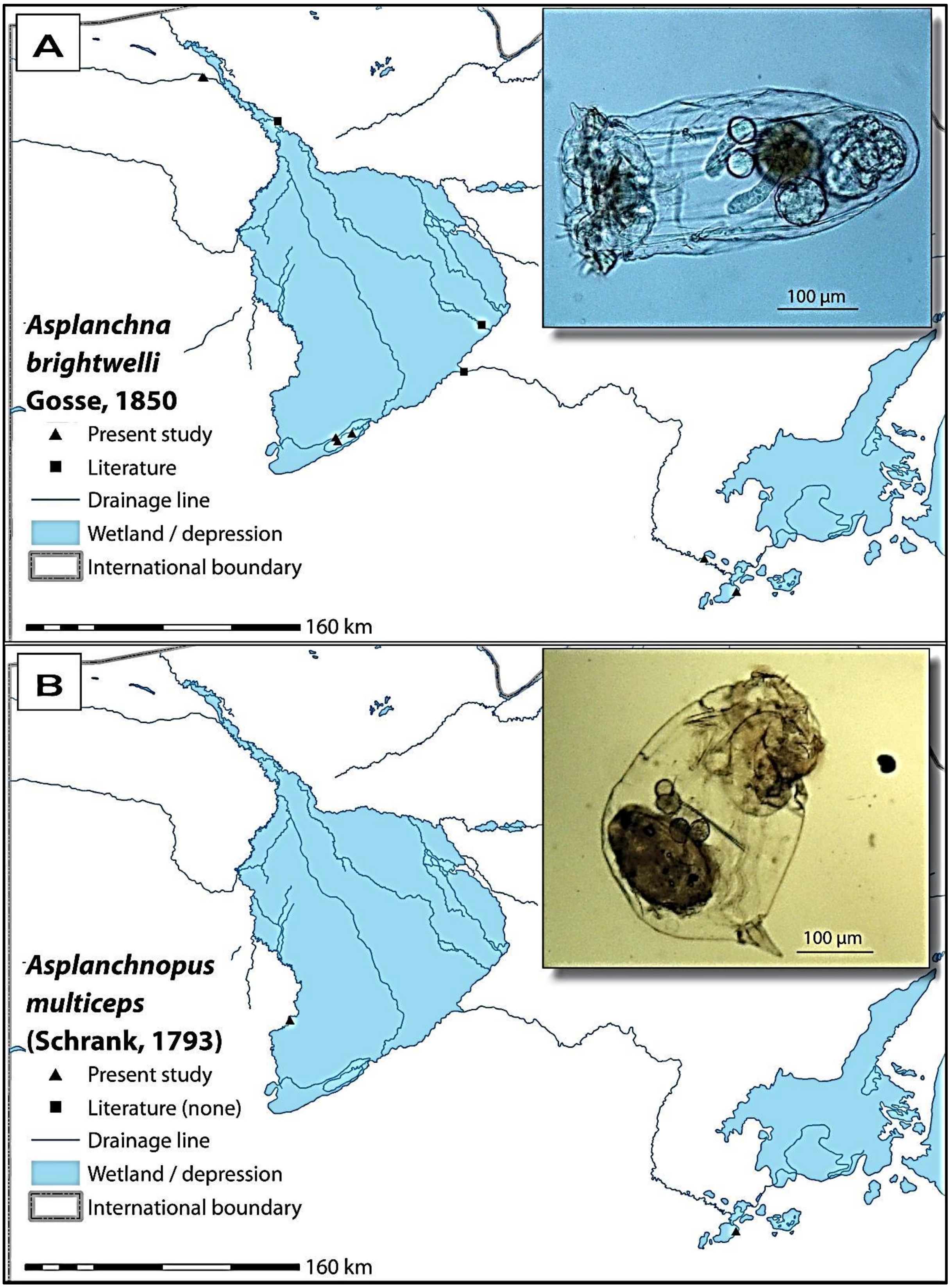

Figure 5.2: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Asplanchna brightwelli* Gosse, 1850 and **B**: *Asplanchnopus multiceps* (Schrank, 1793) throughout the Okavango Delta and its associated basins, Botswana.

FAMILY BRACHIONIDAE Ehrenberg, 1838

The Brachionidae are amongst the most well-studied groups of rotifers, mainly because of their ecological and economic importance (Athibai *et al*. 2013). Eleven species of Brachionidae, belonging to five genera, were identified from the Okavango Delta and its associated basins. Genera included *Anuraeopsis*, *Brachionus*, *Keratella*, *Platyias* and *Trichotria* (Table 5.1). The most diverse genus of the northern Botswana Brachionidae is *Brachionus* comprising six species, followed by *Keratella* with two species (Table 5.1). This corresponds with the statement by Segers (2008) that *Brachionus* is the most diverse genus (64 species) of the Brachionidae worldwide.

Genus *Anuraeopsis* Lauterborn, 1900 (Fig. 5.3)

One species of *Anuraeopsis* was identified, namely *Anuraeopsis fissa* Gosse, 1851. *Anuraeopsis fissa* has previously been sampled from the lower reaches of the Okavango Delta, the Thamalakane River and the upper reaches of the Boteti River. During the present study, *A. fissa* was present in the Thamalakane River (Maun04) and in Lake Xau (LX04) in August 2012 (Table 5.2) (Fig. 5.3). This species has not at all been sampled from the Okavango Panhandle and neither was it present in Lake Ngami during the duration of the present study. The distribution patterns indicate a preference for the seasonally inundated areas within the southern parts of the system.

Genus *Brachionus* Pallas, 1766 (Figs. 5.4A, 5.4B, 5.5A, 5.5B, 5.6A & 5.6B)

The genus *Brachionus* is a diverse group and one of the earliest described genera of monogononts. Its members, which are frequently found in the plankton (Green 2003), are widely distributed throughout all geographical regions worldwide and it is considered to be cosmopolitan. It is no surprise, therefore, that this taxon was the most diverse and widely distributed genus throughout the study area in northern Botswana. The six *Brachionus* species present in the Okavango Delta and its associated basins include *Brachionus angularis* (Fig. 5.4A), *B. budapestinensis* Daday, 1885 (Fig. 5.4B), *B. calyciflorus* (Fig. 5.5A), *B. caudatus* Barrois & Daday, 1894 (Fig. 5.5B), *B. falcatus* Zacharias, 1898 (Fig. 5.6A) and *B. quadridentatus* Herman, 1783 (Fig. 5.6B). These species were generally common and widely distributed throughout the system in all water bodies, with the exception of *B. budapestinensis* (Table 5.2) (Figs. 5.4, 5.5 & 5.6). The latter has been sampled from the temporarily flooded floodplains of the lower delta on one occasion during a previous study (Green 2003) and from the Nxamasere Floodplain (NX02), the Thamalakane River (Maun04) and Lake Xau (LX04) in August and September 2012 during the present study (Figs. 4.1, 4.2, 4.3 & 5.4B).

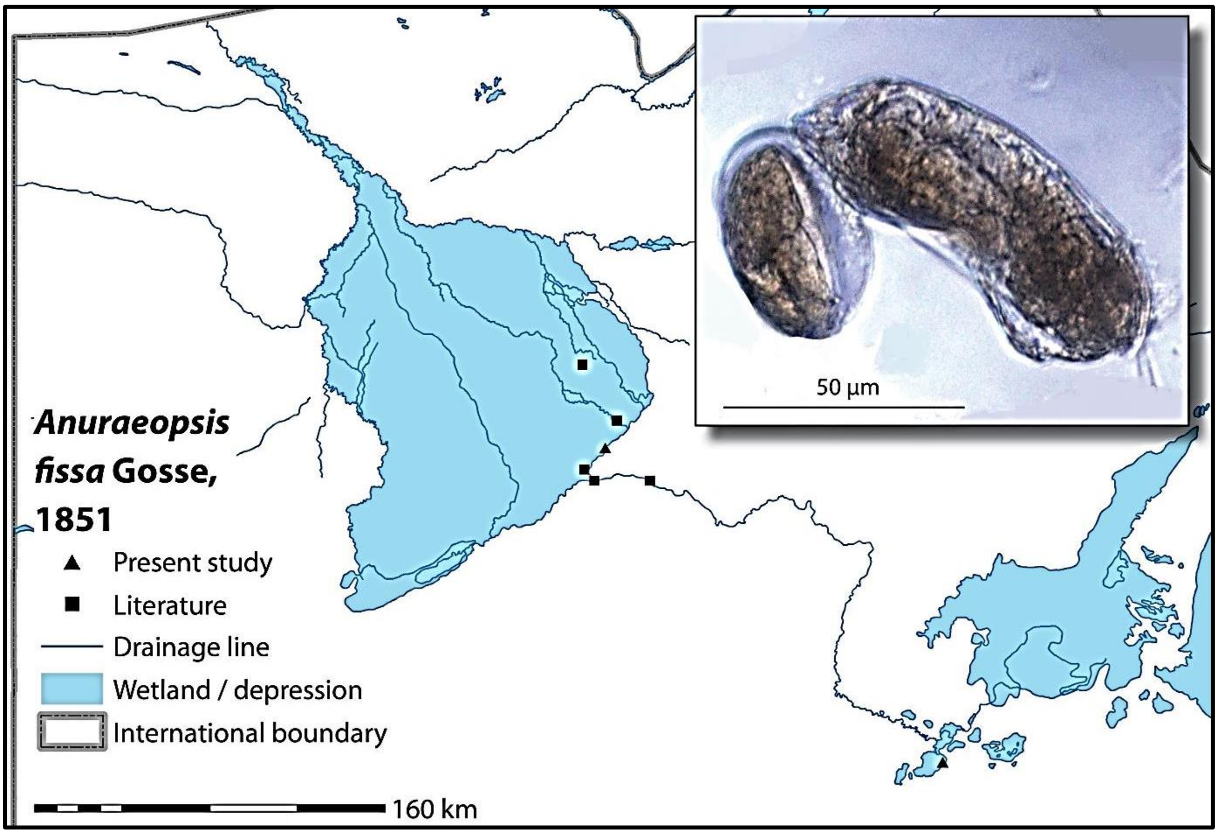

Figure 5.3: Geographic Information System (GIS) maps indicating the distribution of the rotifer *Anuraeopsis fissa* Gosse, 1851 throughout the Okavango Delta and its associated basins, Botswana.

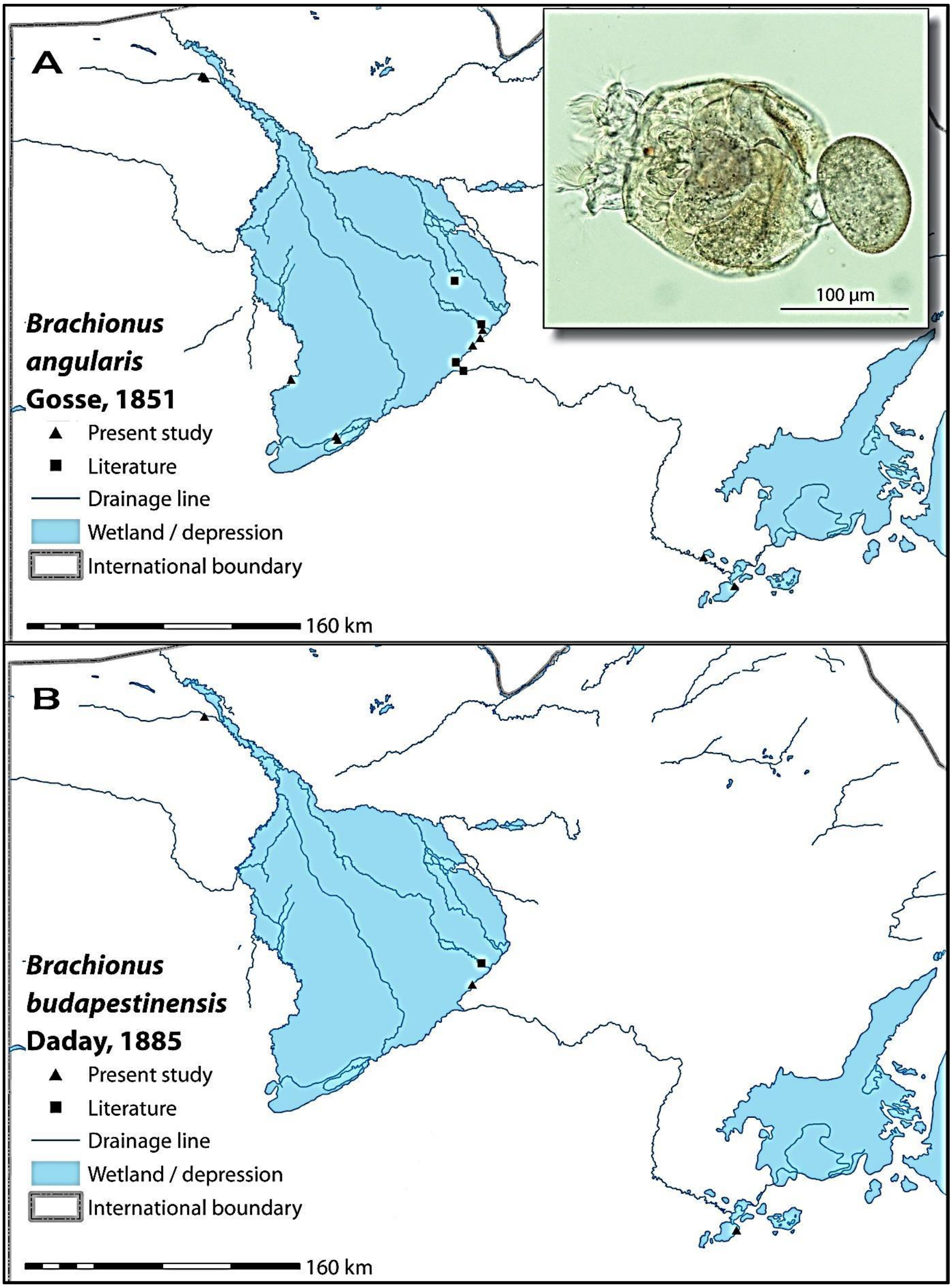

Figure 5.4: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Brachionus angularis* Gosse, 1851 and **B**: *Brachionus budapestinensis* Daday, 1885 throughout the Okavango Delta and its associated basins, Botswana.

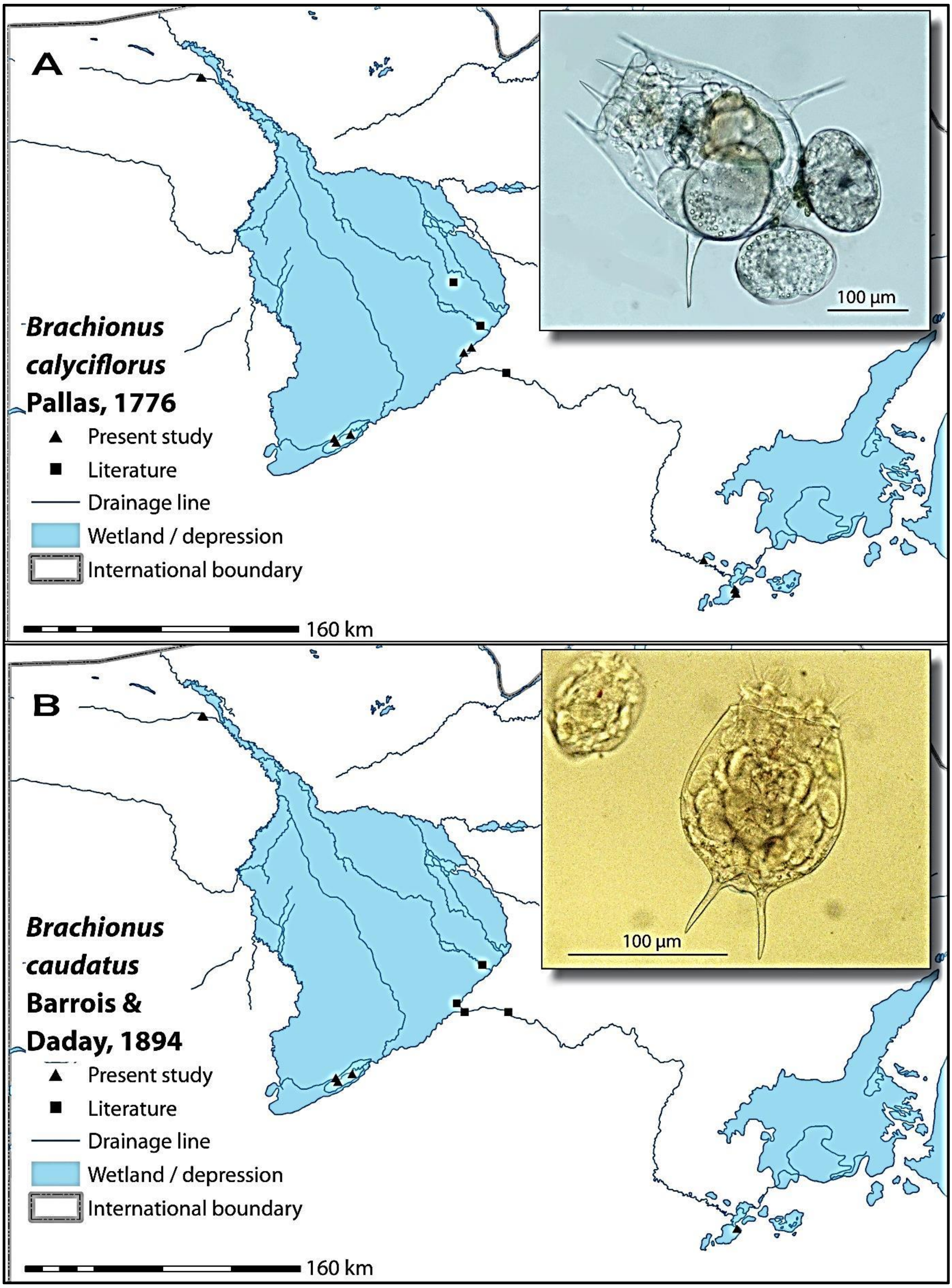

Figure 5.5: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Brachionus calyciflorus* Pallas, 1766 and **B**: *Brachionus caudatus* Barrois & Daday, 1894 throughout the Okavango Delta and its associated basins, Botswana.

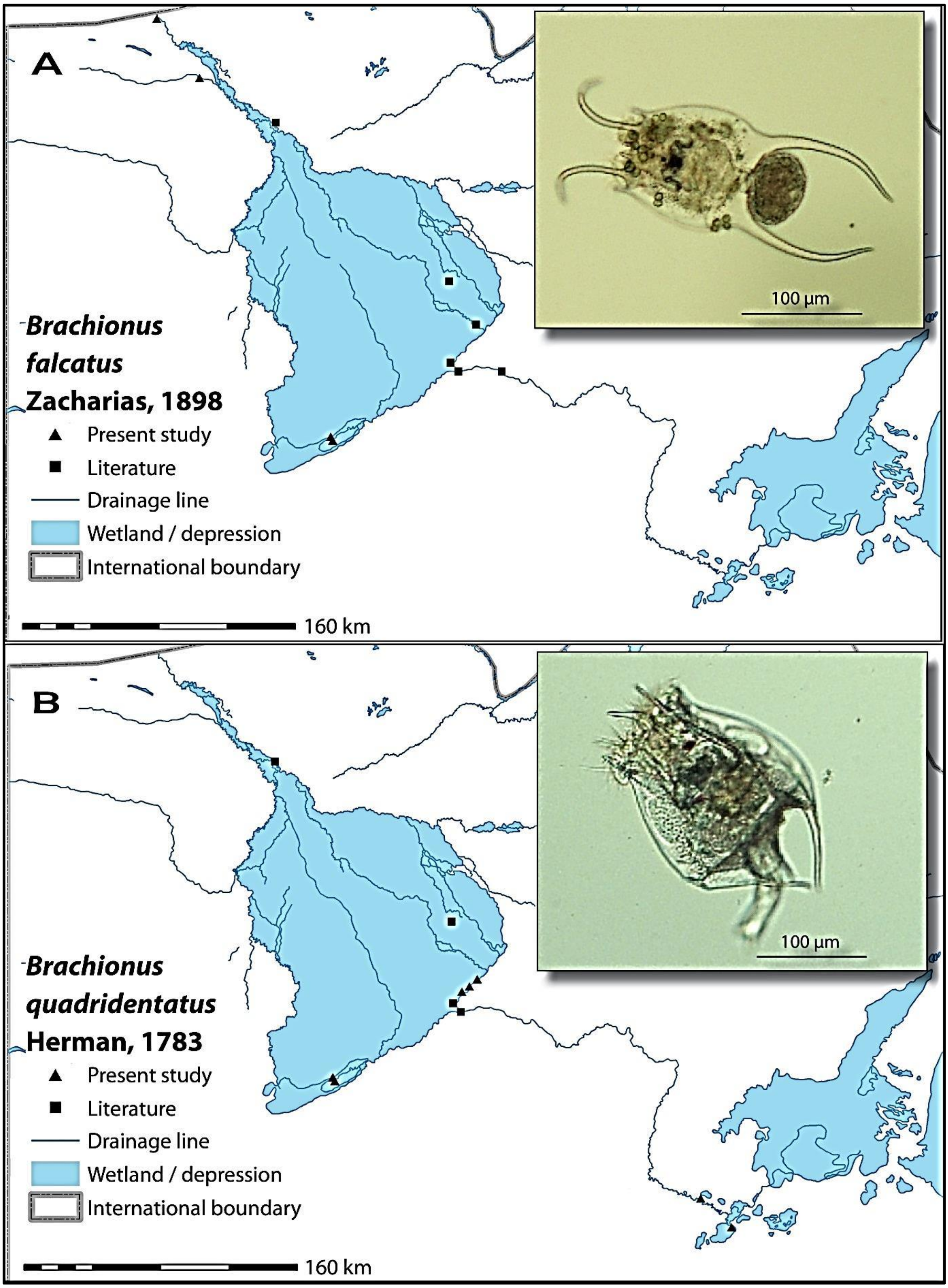

Figure 5.6: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Brachionus falcatus* Zacharias, 1898 and **B**: *Brachionus quadridentatus* Herman, 1783 throughout the Okavango Delta and its associated basins, Botswana.

Genus *Keratella* Bory de St. Vincent, 1822 (Figs. 5.7A & 5.7B)

Species of the genus *Keratella* are planktonic and live in water bodies of various sizes. They are cosmopolitan and have a wide tolerance range for temperature and salinity (Ruttner-Kolisko 1974). *Keratella* was a widely distributed genus throughout the entire study area and was represented by two species. *Keratella tecta* has only once been sampled from the lower Okavango Delta between Chief's Island and the Thamalakane River by Siziba *et al.* (2011). During the present study, however, it was sampled throughout the region, from the Nxamasere Floodplain in the Upper Panhandle to the lower reaches of the delta fan, the Thamalakane River, Lake Ngami, the Boteti River as well as Lake Xau (Fig. 5.7A). In fact it was one of the top four most widely distributed species of the phylum Rotifera present in the Okavango Delta and its associated basins (Table 5.2).

Keratella tropica, together with *B. angularis,* was the most widely distributed species throughout the study region in northern Botswana. It was found in all water bodies during the present study and has also been sampled in a number of regions throughout the delta, Thamalakane River and Boteti River during previous studies (Fig. 5.7B) (Green 2003; Siziba *et al.* 2011). An ecologically important trait of *K. tropica* is that it exhibits environmentally controlled variation in spine development and body size. This may be influenced by temperature, food concentration and the presence of kairomones released by their natural predators such as crustaceans and members of the genus *Asplanchna* (Gilbert & Stemberger 1984; Gilbert 2011). *Keratella tropica* sampled throughout the region displayed a significant spine length (Fig. 5.7B).

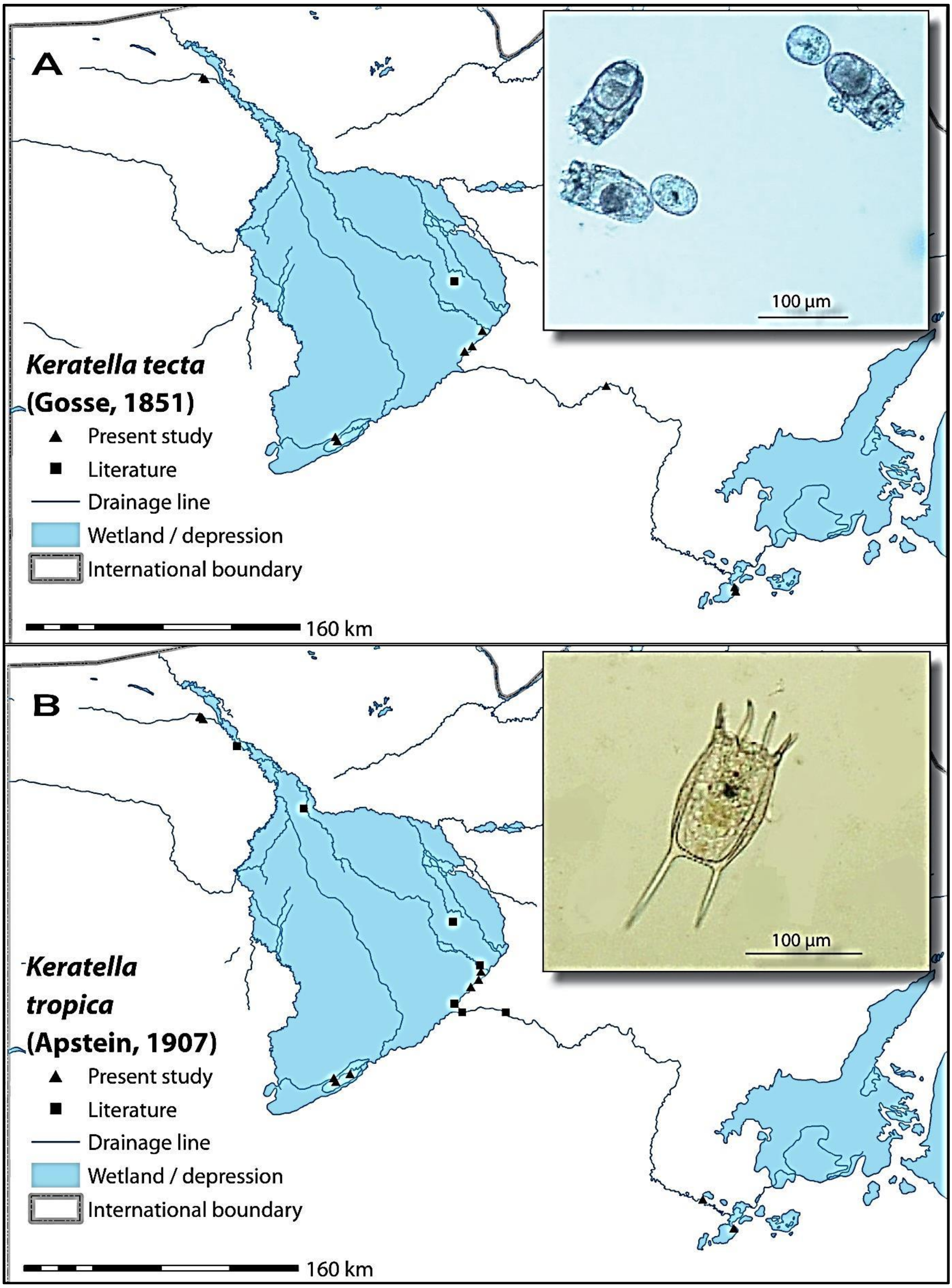

Figure 5.7: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Keratella tecta* (Gosse, 1851) and **B**: *Keratella tropica* (Apstein, 1907) throughout the Okavango Delta and its associated basins, Botswana.

Genus *Platyias* Harring, 1913 (Fig. 5.8A)

The genus *Platyias* is mainly found in warm climates in the littoral zone and amongst macrophytes of either fresh water or slightly saline inland waters. It is never present in large numbers and is sporadically widespread (Ruttner-Kolisko 1974). During the present study, *Platyias quadricornis* was sampled on one occasion only from a site along the Thamalakane River (MaunTJL) in August 2012. It has previously been sampled (Green 2003) from the lower Panhandle as well as the lower reaches of the Okavango Delta, the Thamalakane River and the upper Boteti River just below the confluence of the Thamalakane and Lake Rivers (Fig. 5.8A).

Genus *Trichotria* Bory de St. Vincent, 1827 (Fig. 5.8B)

One species of the genus *Trichotria* was present in the Okavango Delta, namely *Trichotria pocillum* (Müller, 1776). It was not sampled from the Okavango Panhandle during the present study or during previous studies and was neither present in any of the Okavango Delta’s associated basins. It was only sampled once in the upper reaches of the Okavango Delta Fan by Green (2003) and in the most westerly distributary of the delta fan, the Thaoge channel (Thaoge Tsau), and in the Thamalakane River (MaunTJL) in August 2012 during the present study (Fig. 5.8B). It is not surprising that this species was sampled on only a few occasions as members of the genus *Trichotria* are only found as isolated migrants in the plankton and are mainly found in the littoral zone among aquatic plants (Ruttner-Kolisko 1974).

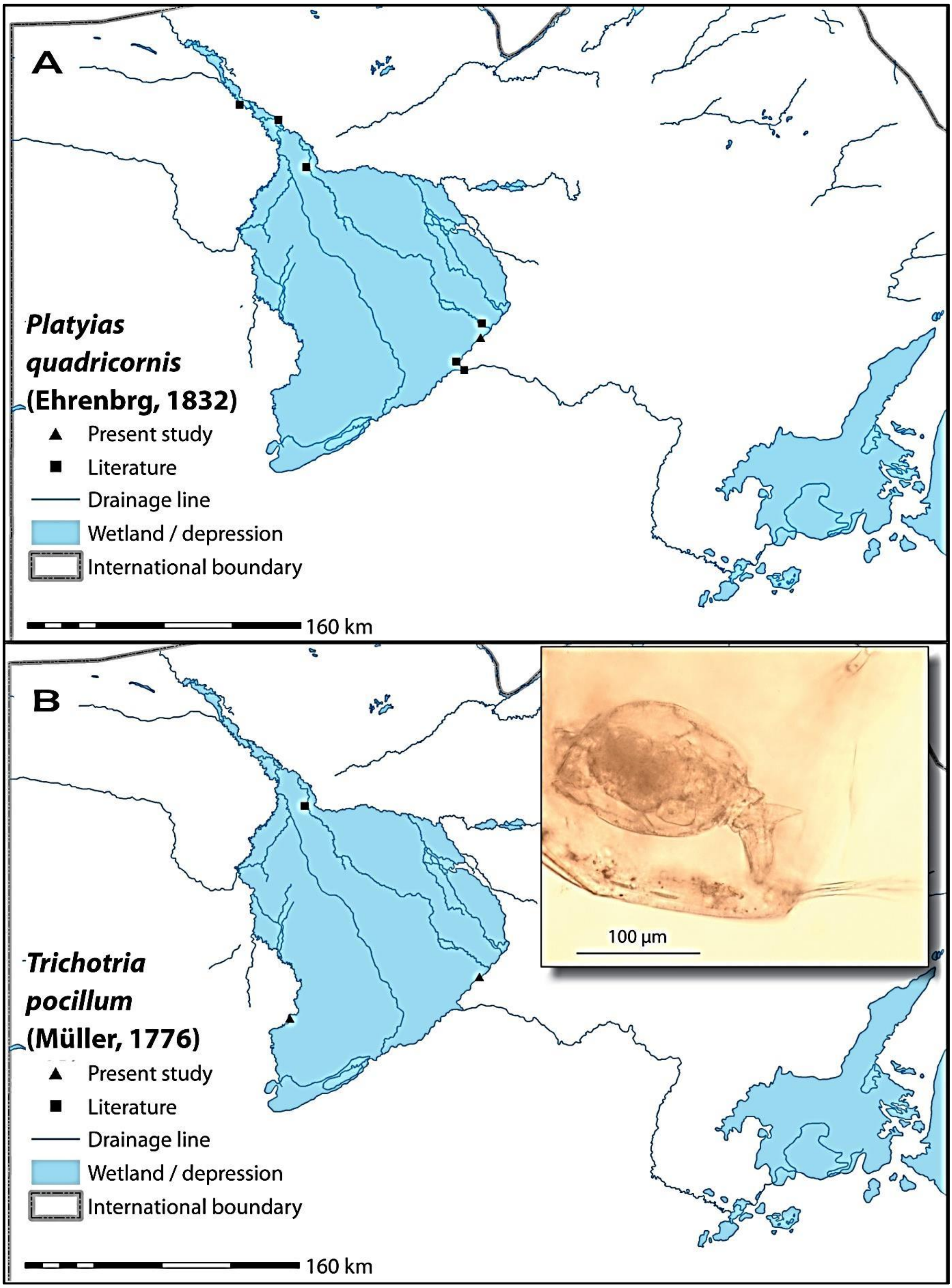

Figure 5.8: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Platyias quadricornis* (Ehrenberg, 1832) and **B**: *Trichotria pocillum* (Müller, 1776) throughout the Okavango Delta and its associated basins, Botswana.

FAMILY COLURELLIDAE Wesenberg-Lund, 1929

Genus *Colurella* Bory de St. Vincent, 1824 (Fig. 5.9)

The family Colurellidae was represented by only one genus (*Colurella*) and one species. *Colurella uncinata* (Müller, 1773) has a widespread distribution, but was not present in either of the lakes (Fig. 5.9). Although Green (2003) collected it from the panhandle, this species was not present in that area throughout the present study. It was, however, sampled from the less frequently flooded lower areas of the system such as the Thaoge Channel (Taoge Tsau), the temporarily flooded areas of the lower Delta (Maun03), the Thamalakane River (Maun04) and the lower reaches of the Boteti River (Xhumo Bridge) in August 2012.

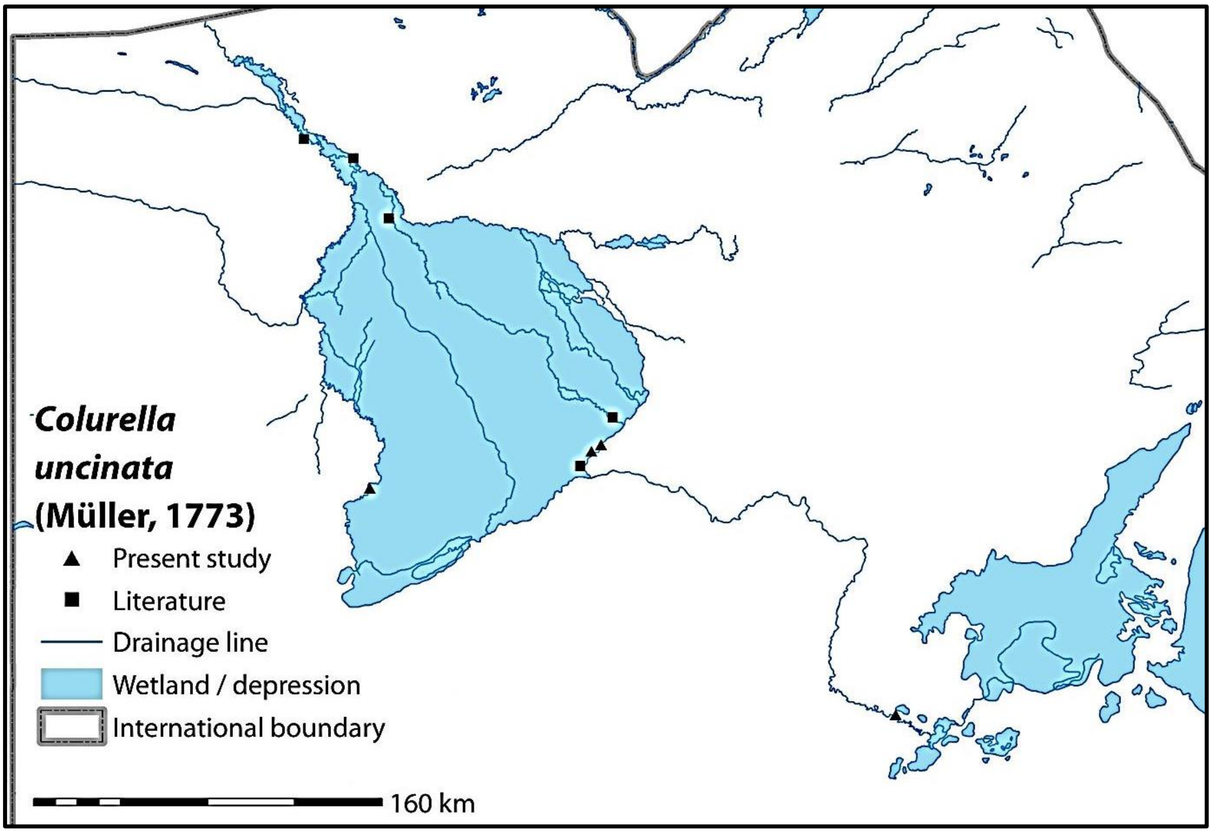

Figure 5.9: Geographic Information System (GIS) maps indicating the distribution of the rotifer *Colurella uncinata* (Müller, 1773) throughout the Okavango Delta and its associated basins, Botswana.

FAMILY EPIPHANIDAE Harring, 1913

Genus *Epiphanes* Ehrenberg, 1832 (Fig. 5.10A)

A single genus and species of the family Epiphanidae, *Epiphanes senta* (Müller, 1773), was collected from the study area at only two sites, namely Thaoge Tsau (in the Thaoge Channel) and Lake Ngami (LN02). Species of the genus *Epiphanes* are typically found in small bodies of water which dry up for extended periods and therefore their development and reproduction are rapid. A single female is able to lay up to 50 eggs, which may develop in less than 24 hours and most species have a short life-cycle and long resting stage. Members of the genus *Epiphanes* prefer feeding on green flagellates, but they do feed on other algae (Ruttner-Kolisko 1974).

This is the first record of *E. senta* in the Okavango Delta and its associated basins (Fig. 5.10A). The resting eggs of *E. senta* are able to endure very long periods of desiccation and the species has a high tolerance level for temperature and salinity. They are often found in polluted pools, cattle troughs, puddles of liquid manure and desert water-holes, amongst others (Ruttner-Kolisko 1974). Their high tolerance, rapid life-cycle and effective production of resistant overwintering eggs would explain their success in an area which experienced only one season of flooding (August 2012) in decades, namely the Thaoge Channel (Thaoge Tsau).

FAMILY EUCHLANIDAE Ehrenberg, 1838

Genus *Euchlanis* Ehrenberg, 1832 (Fig. 5.10B)

Like many of the families present in the Okavango Delta and its associated basins, Euchlanidae was represented by only one species - *Euchlanis dilatata* Ehrenberg, 1832. The populations of *E. dilatata* were only represented by a few individuals, although it was distributed throughout the study area, except in the two lakes – Ngami and Xau. It was sampled in the Nxamasere Floodplain (NX01) in the upper panhandle, the Thamalakane River (Maun04) as well as the lower Boteti River (Xhumo Bridge) (Table 5.2) during the present study and in the lower panhandle, the Okavango Delta Fan and the upper Boteti River by previous authors such as Green (2003) and Siziba *et al.* (2011).

Euchlanis dilatata is a cosmopolitan species which is often also present in saline water. It is not only present in the plankton, but is common among macrophytes in the littoral zone (Ruttner-Kolisko 1974).

FAMILY LECANIDAE Remane, 1933

Genus *Lecane* Nitzsch, 1827 (Figs. 5.11A & 5.11B)

The famiy Lecanidae is represented by one genus, *Lecane*, and two species, one of which was amongst the top five most widely distributed species in the system. *Lecane bulla* (Gosse, 1851) was present in all the water bodies (Table 5.2) during the present study, except in Lake Xau (Fig. 5.11A). It was, however, collected just north of Lake Xau in a floodplain along the Boteti River (Xhumo Bridge) (Fig. 5.11A). Green (2003) also sampled *L. bulla* throughout his study area and Siziba *et al.* (2011) reported it from their study site south of Chief's Island in the Okavango Delta Fan. In the genus *Lecane, L. bulla* is one of the most widespread species, mainly in the tropics and subtropics. It occurs abundantly in the plankton of shallow lakes and often attaches to blue-green algae (Green 2003).

It is believed that species of the genus *Lecane* are benthic and that they are only found in the plankton as "occasional migrants" (Ruttner-Kolisko 1974). The opposite seems to be true for *L. bulla*, since it was easily sampled throughout the Okavango Delta and its associated basins during the present study and previous studies (Green 2003; Siziba *et al.* 2011) by making use of classic hand-held plankton nets.

Lecane papuana (Murray, 1913), although less frequently encountered, also shows a wide distribution range. It too was not present in Lake Xau and was only sampled from the upper panhandle, Lake Ngami and the lower Boteti River during the present study. Green (2003), however, recorded it from the lower delta fan, the Thamalakane River and the upper Boteti, hence increasing its distribution range (Fig. 5.11B).

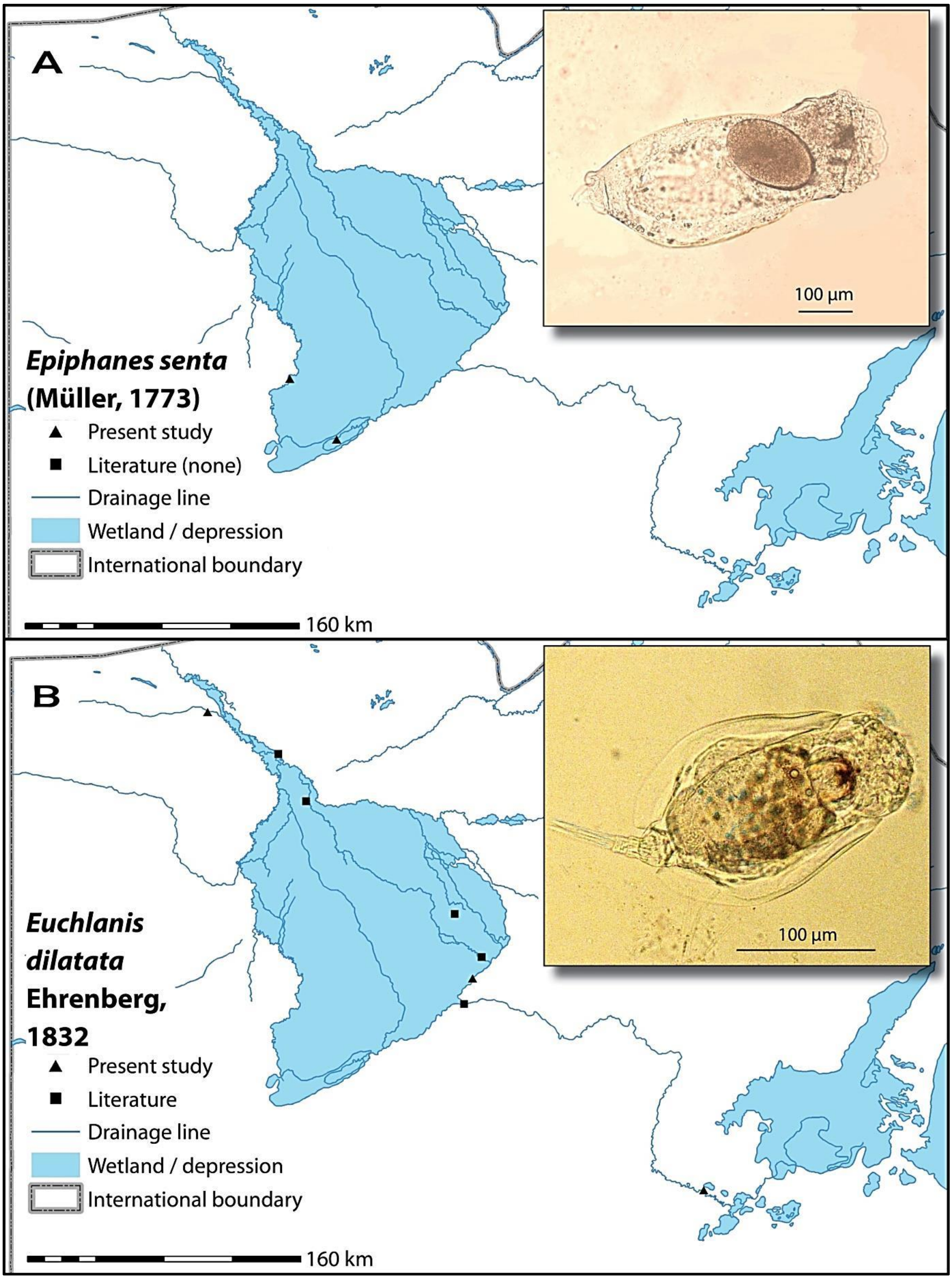

Figure 5.10: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Epiphanes senta* (Müller, 1773) and **B**: *Euchlanis dilatata* Ehrenberg, 1832 throughout the Okavango Delta and its associated basins, Botswana.

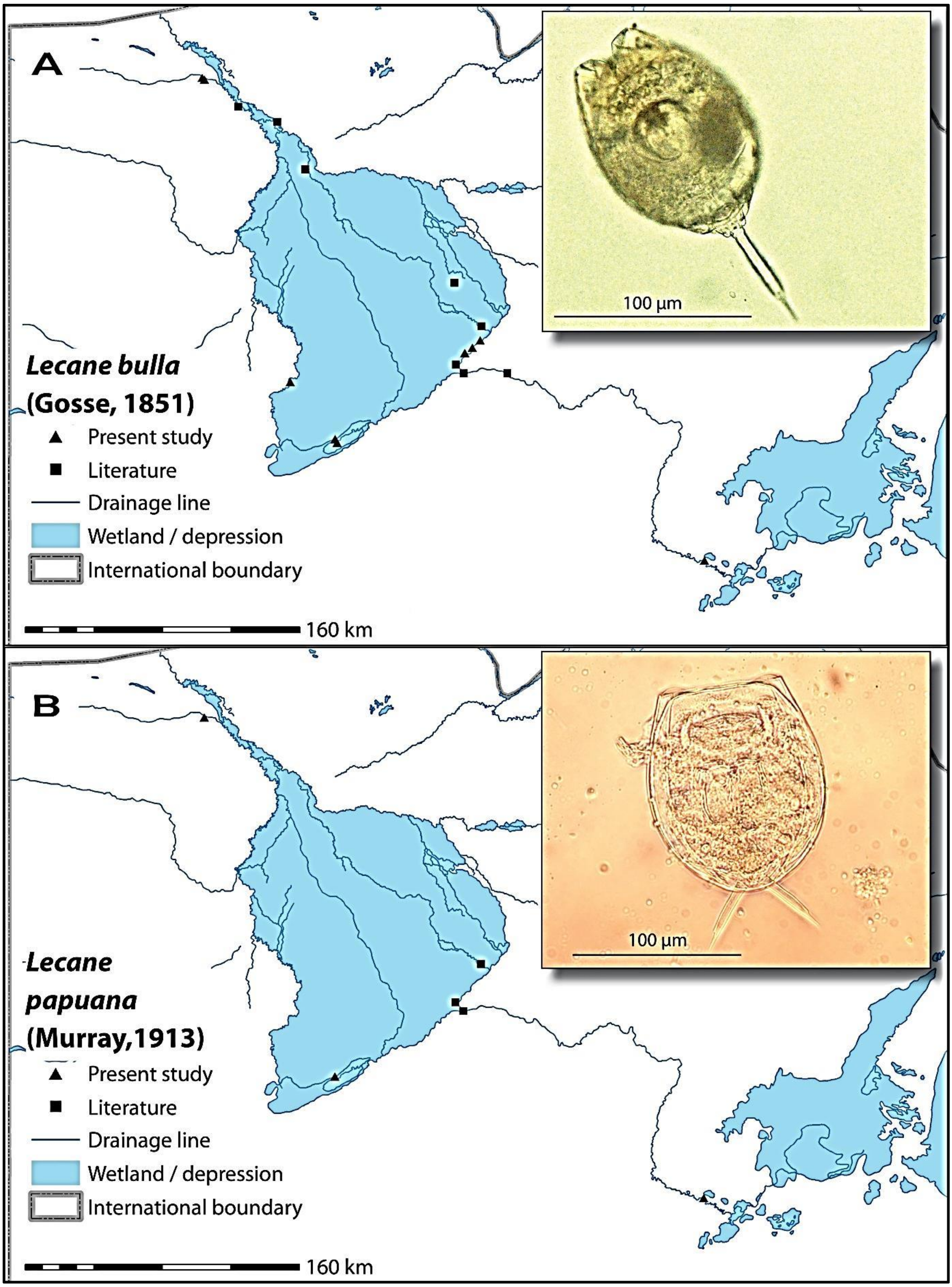

Figure 5.11: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Lecane bulla* (Gosse, 1851) and **B**: *Lecane papuana* (Murray, 1913) throughout the Okavango Delta and its associated basins, Botswana.

FAMILY NOTOMMATIDAE Hudson & Gosse, 1886

Genus *Monommata* Bartsch, 1870 (Fig. 5.12)

Monommata grandis Tessin, 1890 was the only representative of the family Notommatidae. It was sampled at two study sites during the course of the study. The first was in the Thamalakane River (Maun04) in August 2012 and the second in the Nxamasere Floodplain (NX07) in July 2013. Green (2003) also collected *M. grandis* from the Okavango Delta (Fig. 5.12).

Although cosmopolitan, this species is considered to be very rare with single finds in lentic waters of North America (Błędzki & Ellison 2003), Europe (Ejsmont-Karabin & Kuczyńska-Kippen 2001; Streletskaya 2010), Asia (Trinh Dang *et al.* 2013) and the South Pacific Islands (Russell 1957). It also is an indicator of oligosaprobic conditions (Virro & Haberman 2005), as it prefers waters with low amounts of organic waste.

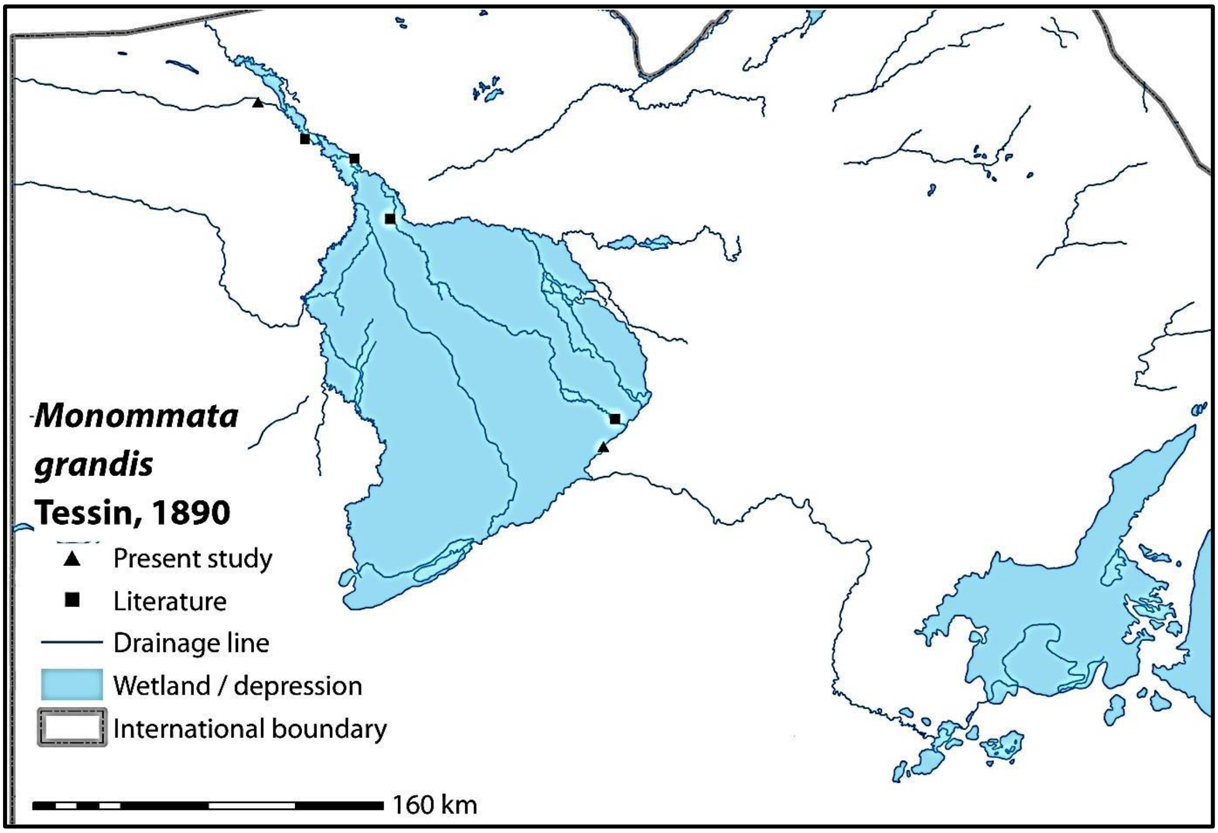

Figure 5.12: Geographic Information System (GIS) maps indicating the distribution of the rotifer *Monommata grandis* Tessin, 1890 throughout the Okavango Delta and its associated basins, Botswana.

FAMILY SYNCHAETIDAE Hudson & Gosse, 1886

The family Synchaetidae was represented by two genera, namely *Polyarthra* and *Synchaeta*.

Genus *Polyarthra* Ehrenberg, 1834 (Fig. 5.13A)

The only species of the genus *Polyarthra* present, *Polyarthra remata* Skorikov, 1896, was collected in the northern panhandle at Mohembo (Mohembo Pool) in 2012 and in the Nxamasere Floodplain (NX06, NX07 & NX11) in 2013. It was also collected from Lake Ngami (LN02) on one occasion in August 2012. Previous studies (Green 2003; Siziba *et al*. 2011), however, place this species in the Okavango Delta Fan (lower Boro River and south of Chief's Island) and the Thamalakane River (Fig. 5.13A). It has not been recorded from water bodies south of the Thamalakane such as the Boteti River and Lake Xau. This is a planktonic species normally found in the littoral zone of alkaline to neutral, warm water bodies (Ruttner-Kolisko 1974).

Genus *Synchaeta* Ehrenberg, 1832 (Fig. 5.13B)

The genus *Synchaeta* comprises more or less 30 species of doubtful taxonomic validity. Most species are found in marine or brackish environments and only a small number are confined entirely to freshwater (Ruttner-Kolisko 1974). *Synchaeta pectinata* was collected on one occasion from a single study site (Fig. 5.13B). It was sampled in the lower Boteti River at Xhumo Bridge in August 2012. This is the first record of the genus and species from the waterways of northern Botswana. Both *Synchaeta* and *Asplanchnopus* (which was also reported for the first time), were sampled from areas which have not been inundated for decades.

Ruttner-Kolisko (1974) and Obertegger *et al*. (2006) point out that members of the genus *Synchaeta* are rarely identified up to species level in ecological studies as their general morphology is distorted by fixatives. Ruttner-Kolisko (1974) went as far as to say that the genus "must be considered not identifiable in the preserved state". In the present study it was possible to identify this species due to the photomicrographs taken of live specimens before preservation. Photomicrographs, however, were taken of live specimens throughout the study area and despite this, *S. pectinata* was not observed in any area other than at Xhumo Bridge.

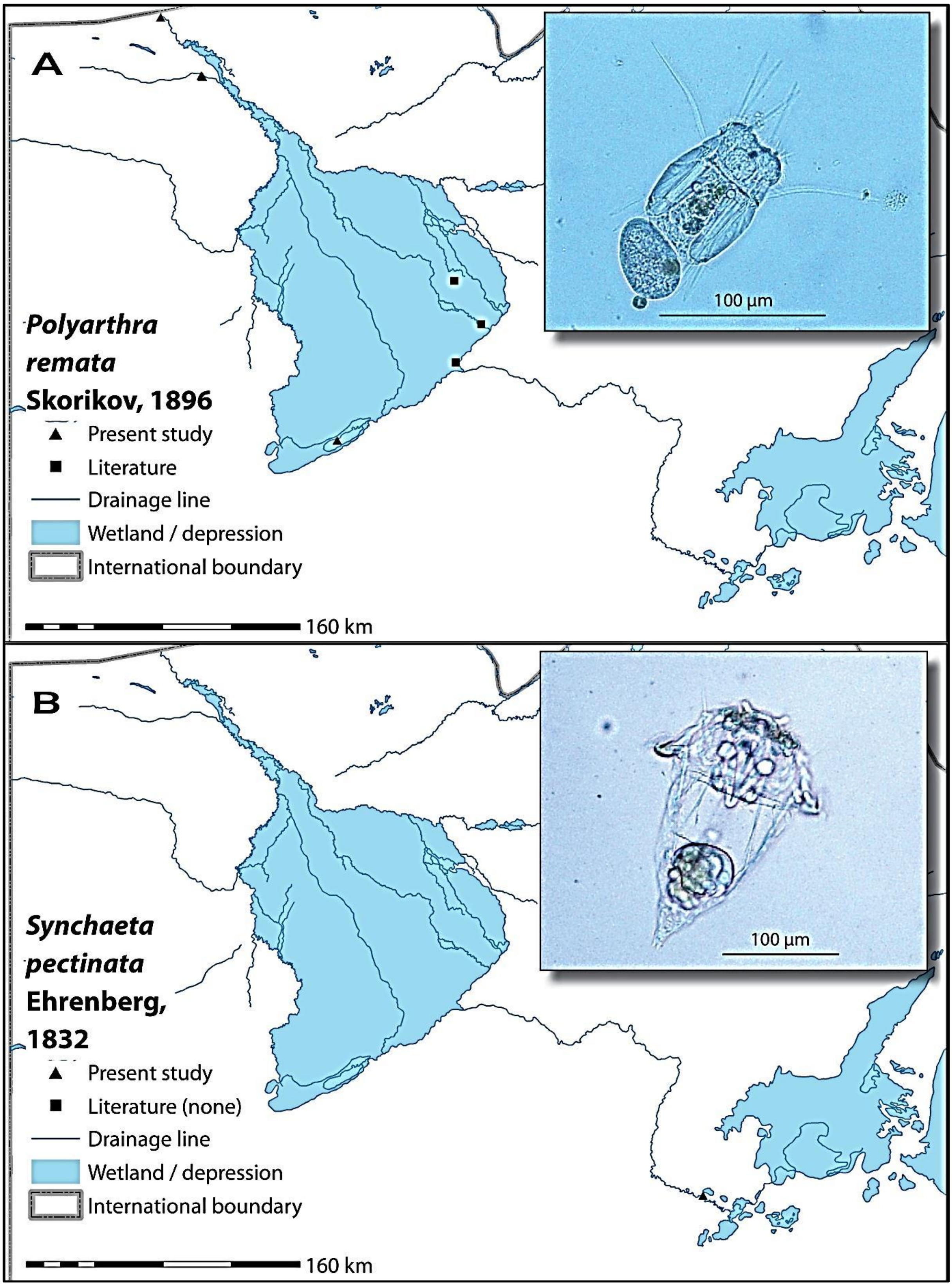

Figure 5.13: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Polyarthra remata* Skorikov, 1896 and **B**: *Synchaeta pectinata* Ehrenberg, 1832 throughout the Okavango Delta and its associated basins, Botswana.

FAMILY TRICHOCERCIDAE Harring, 1913

Genus *Trichocerca* Lamarck, 1801 (Figs. 5.14A, 5.14B & 5.15)

The family Trichocercidae was represented by one genus (*Trichocerca*) and three species. These included *Trichocerca chattoni* (de Beauchamp, 1907) (Fig. 5.14A), *T. elongata* (Gosse, 1886) (Fig. 5.14B) and *T. pusilla* (Fig. 5.15). The former two species have a widespread distribution across the Okavango Delta and its associated basins (Figs. 5.14A & 5.14B), while the latter was only sampled in the Nxamasere Floodplain at NX04 (in 2012) and NX07 (in 2013) (Fig. 5.15) (Table 5.2). Previous studies reported on the presence of *T. pusilla* in the lower Okavango Delta Fan, the Thamalakane River and the Upper Boteti River (Green 2003; Siziba *et al*. 2011).

Trichocerca chattoni was present in the Upper Panhandle (NX04), the Thamalakane River (Maun04), Lake Ngami (LN01 and LN02) and Lake Xau (LX05) in 2012. It was also collected in the lower panhandle at Seronga Lagoon (Hart 1997), the lower Okavango Delta Fan (Green 2003; Siziba *et al*. 2011), the Thamalakane River (Green 2003) and the Upper Boteti River (Green 2003) during previous studies (Fig. 5.14A).

Trichocerca elongata's distribution range overlaps with that of *T. chattoni*. It, too, was sampled from the Upper Panhandle (NX03 in 2013), the Thamalakane River (Maun04 and MaunTJL in 2012), Lake Ngami (LN01 in 2013) and Lake Xau (LX05 in 2012) during the present study. Previous studies also recorded *T. elongata* from the Okavango Delta Fan (Green 2003; Siziba *et al*. 2011) and the Thamalakane and Boteti Rivers (Green 2003) (Fig. 5.14B).

Endemism seems to be rare amongst *Trichocerca* taxa and the majority are considered to be cosmopolitan with a wide distribution range. *Trichocerca chattoni* appears to be confined to warmer waters, while *T. elongata* and *T. pusilla* are cosmopolitan (Segers 2003).

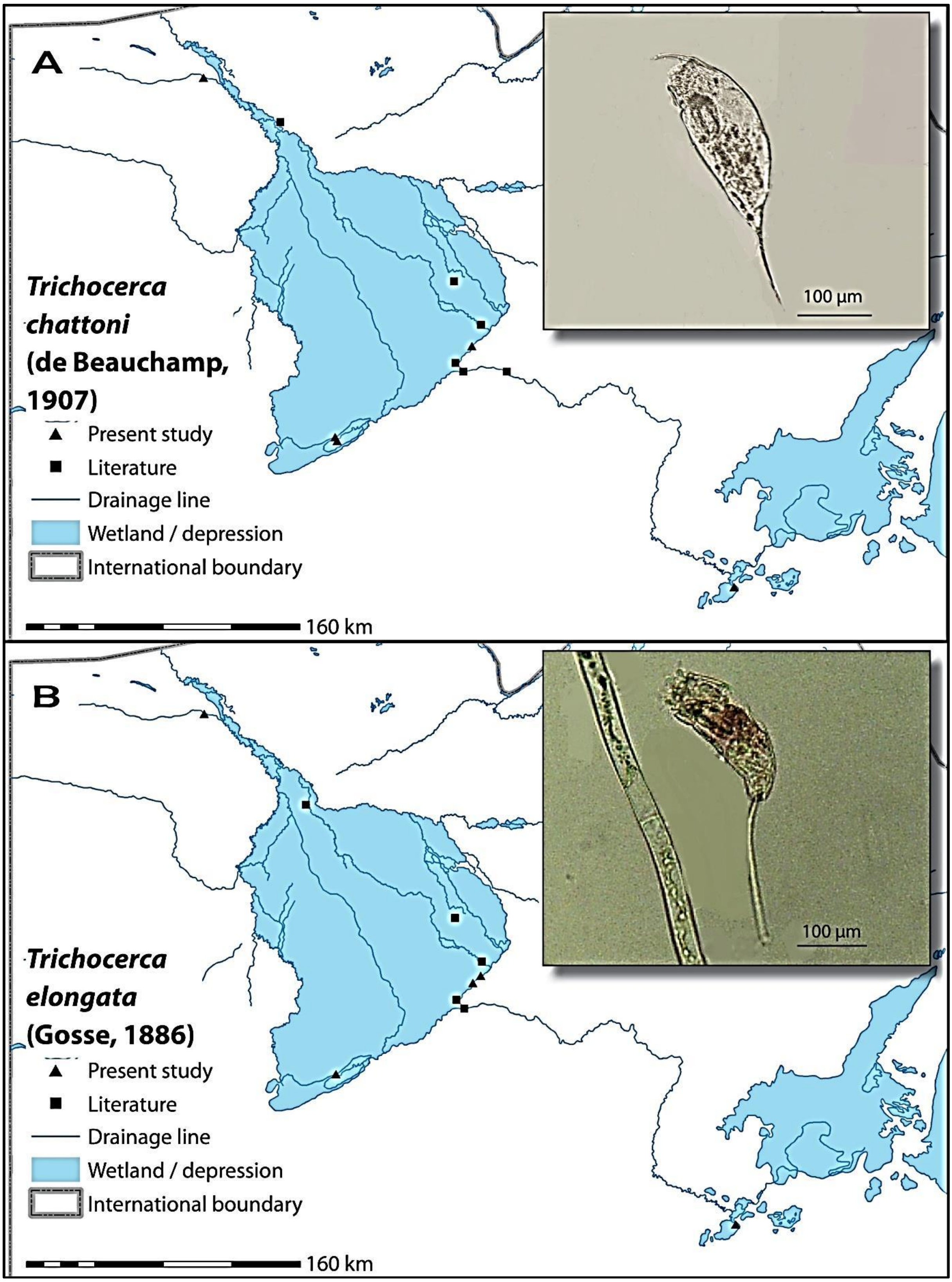

Figure 5.14: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A**: *Trichocerca chattoni* (de Beauchamp, 1907) and **B**: *Trichocerca elongata* (Gosse, 1886) throughout the Okavango Delta and its associated basins, Botswana.

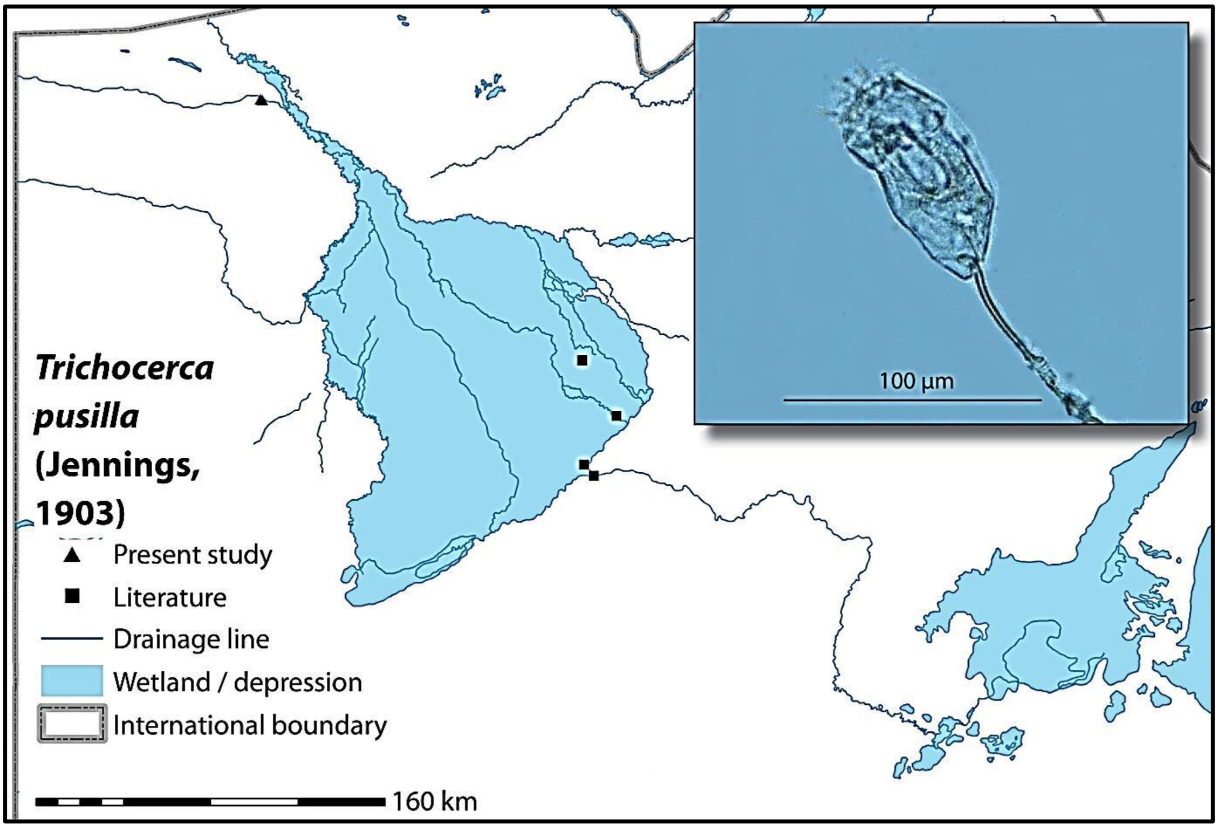

Figure 5.15: Geographic Information System (GIS) maps indicating the distribution of the rotifer *Trichocerca pusilla* (Jennings, 1903) throughout the Okavango Delta and its associated basins, Botswana.

ORDER FLOSCULARIACEA

The order Flosculariacea contains more or less 25 species of colonial rotifers and is the only order with representatives that form colonies (Hochberg 2006). Coloniality is limited to two families within this order, namely Conochilidae and Flosculariidae (Wallace 1987). In the Okavango and its associated basins the Flosculariacea was the second most dominant order with representatives from five families, six genera and eight species (Table 5.1).

FAMILY CONOCHILIDAE Harring, 1913

The family Conochilidae is cosmopolitan and includes less than a dozen described freshwater species from two recognised genera, namely *Conochilus* and *Conochiloides* Hlava, 1904, although some authors do not consider them to be separate genera (Segers & Wallace 2001). Members of the Conochilidae form colonies (Wallace 1987) and in the present study were represented by one genus (*Conochilus*) and two species.

Genus *Conochilus* Ehrenberg, 1834 (Figs. 5.16A & 5.16B)

Colonies of the genus *Conochilus* may be sessile and highly selective of the substratum they attach to or they live and move in the plankton where they auto-recruit. Morphological differences between the two are few. Furthermore, the genus also contains solitary species (Hochberg 2006). The colonial species of *Conochilus* are classified under 'Type II colony formation' which means that the larvae do not have a free-swimming phase, but that they directly accumulate into their parent colony (Wallace 1987). Unfortunately, little is known of the natural ecology of *Conochilus*, except that they are microphagous and mainly feed on small particles of detritus with associated bacteria (Wallace & Starkweather 1985; Hampton 2005).

The two species of the genus *Conochilus* sampled from the Okavango Delta represent a solitary species, *C. dossuarius* Hudson, 1875, and a planktonic, colonial species, *C. unicornis* Rousselet, 1892. This is the first record for both these species in the waterways of northern Botswana. They were only sampled from the Okavango Delta itself and were not found in its associated basins.

Conochilus dossuarius was present in the lower reaches of the Okavango Delta Fan (Maun03) and in the Thamalakane River (MaunTJL) in August 2012 and in the Nxamasere Floodplain (NX03) in July 2013 (Table 5.2) (Fig. 5.16A). As *C. dossuarius* is solitary and sessile, it is not surprising that it was not sampled more often with a plankton net. It is a cosmopolitan species which normally occurs in pools and shallow water (Ruttner-Kolisko 1974) such as the areas it was collected from in the Okavango Delta.

Conochilus unicornis was sampled from the panhandle only, in the Nxamasere Floodplain (NX06, NX07) and the Ngarangi Channel in July 2013 (Fig. 5.16B). This species was present in areas with a longer period of inundation and was found to be highly seasonal. *Conochilus unicornis* is normally found in oligotrophic waters

(Ruttner-Kolisko 1974) with low nutrient levels, low algal production, clear water and high drinking water quality such as that of the Okavango Panhandle (West *et al*. 2015). They generally form colonies of between five and 20 individuals, but colonies of more than 150 individuals have been reported (Wallace 1987).

FAMILY FILINIIDAE Bartoš, 1959

The Filiniidae family was represented by two species, both of the genus *Filinia*.

Genus *Filinia* Bory de St. Vincent, 1824 (Figs. 5.17A & 5.17B)

Filinia longiseta (Ehrenberg, 1834) is a common, cosmopolitan rotifer which is found in the plankton and feeds on detritus, bacteria and *Chlorococcales* (green algae) (Basińska *et al*. 2010). This species is associated with warm and unshaded water bodies (Ruttner-Kolisko 1974) such as those from which it was sampled in the Okavango Delta and its associated lakes. During the present study it was collected from the panhandle (NX07 & NX11) in 2013 and from the Thamalakane River (MaunTJL), Lake Ngami (LN01 & LN02) and Lake Xau (LX05) in 2012. It has previously been sampled from the lower delta fan (Green 2003; Siziba *et al*. 2011), the Thamalakane River (Green 2003) and the Boteti River (Green 2003) (Fig. 5.17A). It is known that *F. longiseta* is a reliable indicator of eutrophic water (Basińska *et al*. 2010), but the opposite is true in this case as the waters of the Okavango Delta are not eutrophic.

Unlike *F. longiseta*, *F. opoliensis* (Zacharias, 1898) was not present in Lake Ngami or Lake Xau. Instead, it was only sampled from the Okavango Delta during the present study. In the panhandle, *F. opoliensis* was collected from the Mohembo Pool and the Nxamasere Floodplain (NX03) in 2012. It was also collected on one occasion in the lower delta fan at Maun05 in 2012. Green (2003) collected it from the lower delta fan, the Thamalakane River and the Boteti River (Fig. 5.17B).

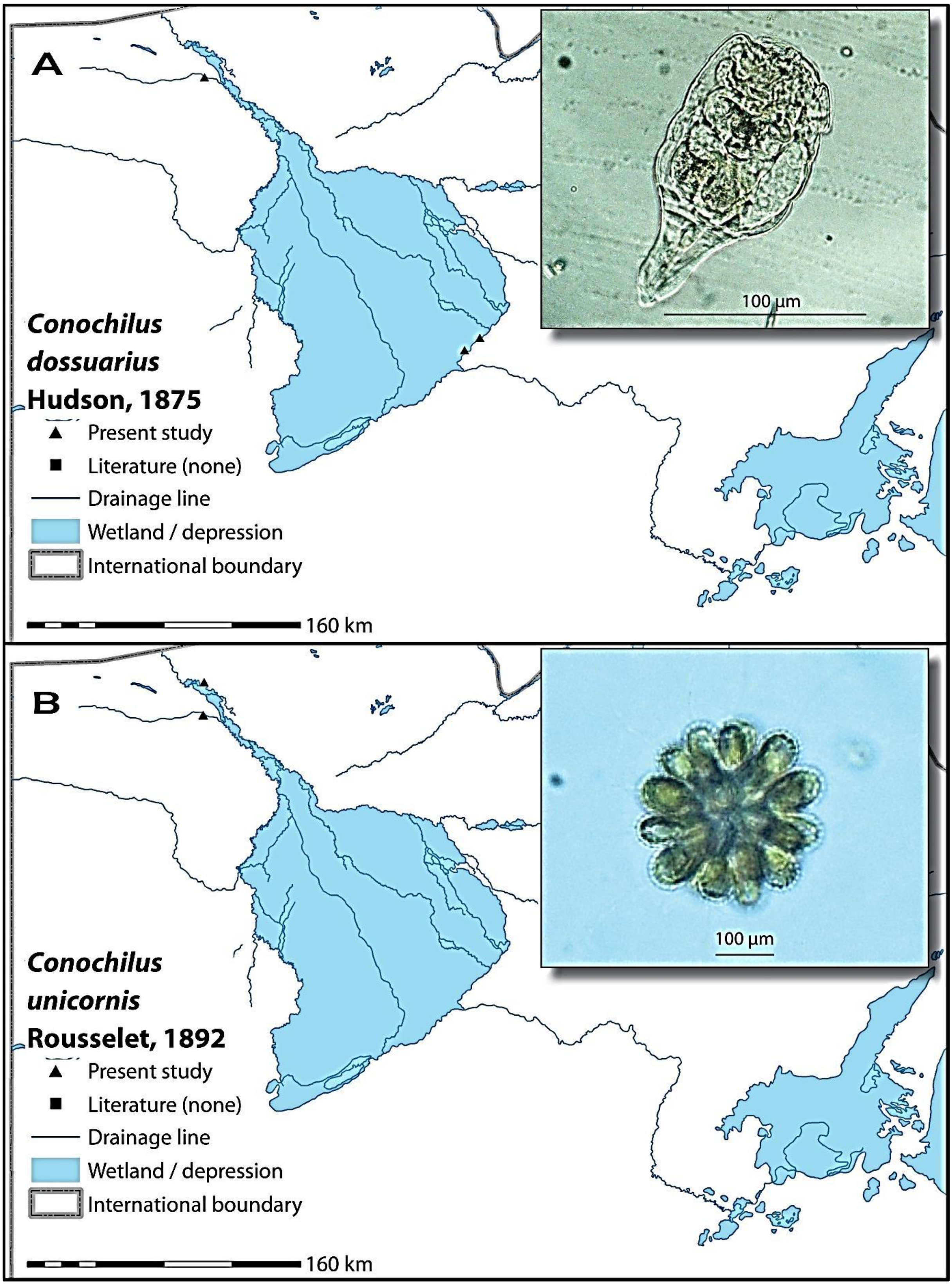

Figure 5.16: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A:** *Conochilus dossuarius* Hudson, 1875 and **B**: *Conochilus unicornis* Rousselet, 1892 throughout the Okavango Delta and its associated basins, Botswana.

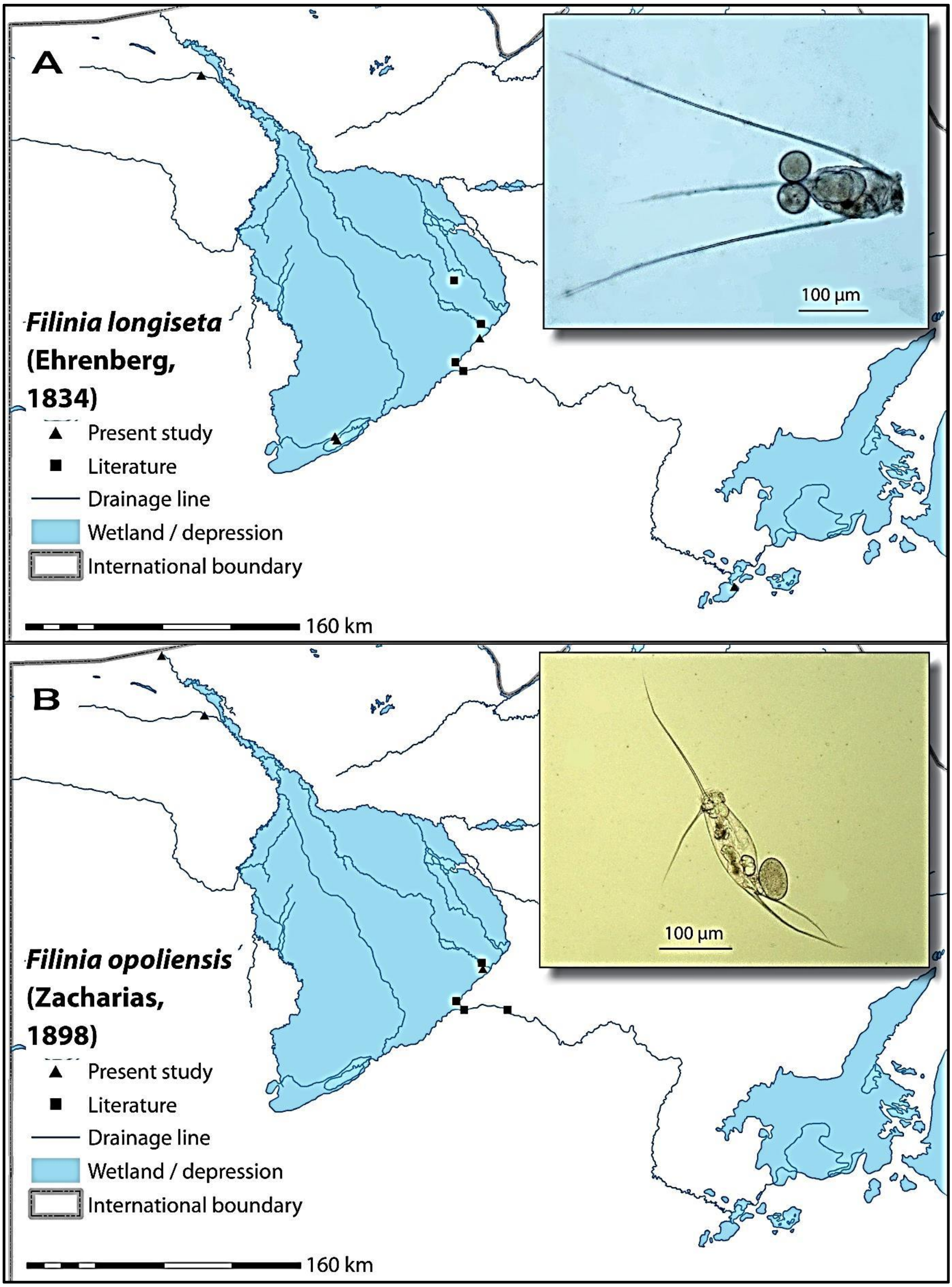

Figure 5.17: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A:** *Filinia longiseta* (Ehrenberg, 1834) and **B**: *Filinia opoliensis* (Zacharias, 1898) throughout the Okavango Delta and its associated basins, Botswana.

FAMILY FLOSCULARIIDAE Ehrenberg, 1838

For members of the family Flosculariidae, as with the family Conochilidae, coloniality seems to be an evolutionary stable strategy in terms of energetic advantage, predator avoidance and the induction of sexuality (Wallace 1987). Wallace (1987) provided an in-depth discussion on these hypotheses. The Flosculariidae were represented by two genera (*Floscularia* and *Sinantherina*) and two species in the Okavango Delta and its associated basins.

Genus *Floscularia* Cuvier, 1798 (Fig. 5.18A)

Members of the genus *Floscularia* are colonial, their activities classified under 'Type I colony formation' by Wallace (1987). This type of colony formation involves free-swimming larvae which select the tubes of settled adults as substrata (Fig. 5.19A). This active substrate selection, implies that the larvae have been recruited to the colony (Wallace 1987). See **Genus *Conochilus* Ehrenberg, 1834** for an explanation of 'Type II colony formation'. Members of this genus are also sessile and use detritus to form pellets which they arrange like bricks into a small tower to build a tube (Figs. 5.19B, 5.19C & 5.19D) (Wallace 1987; Santo *et al*. 2005).

Floscularia ringens was sampled on one occasion in 2013 from the Nxamasere Floodplain (NX03). It was previously sampled from the Okavango Panhandle and upper reaches of the Okavango Delta Fan by Green (2003) (Fig. 5.18A). Figure 5.19 illustrates what the *F. ringens* colonies (Fig. 5.19A) looked like in the Nxamasere floodplain as well as their tube formation (Figs. 5.19B & 5.19C). An individual that vacated its tube is also illustrated in Figures 5.19D, 5.19E and 5.19F.

Genus *Sinantherina* Bory de St. Vincent, 1826 (Fig. 5.18B)

An unidentified species of the genus *Sinantherina* was sampled from the Nxamasere Floodplain (NX07) in the Upper Panhandle in July 2013 (Fig. 5.18B). This is the first record of the genus *Sinantherina* from the waterways of northern Botswana. *Sinantherina* is a colonial rotifer classified under 'Type II colony formation' together with the colonial species of *Conochilus* (Wallace 1987). Like the colonial *Conochilus* species, *Sinantherina* colonies are planktonic and do not build tubes (Wallace 1987) and are not sessile such as the *Floscularia* colonies.

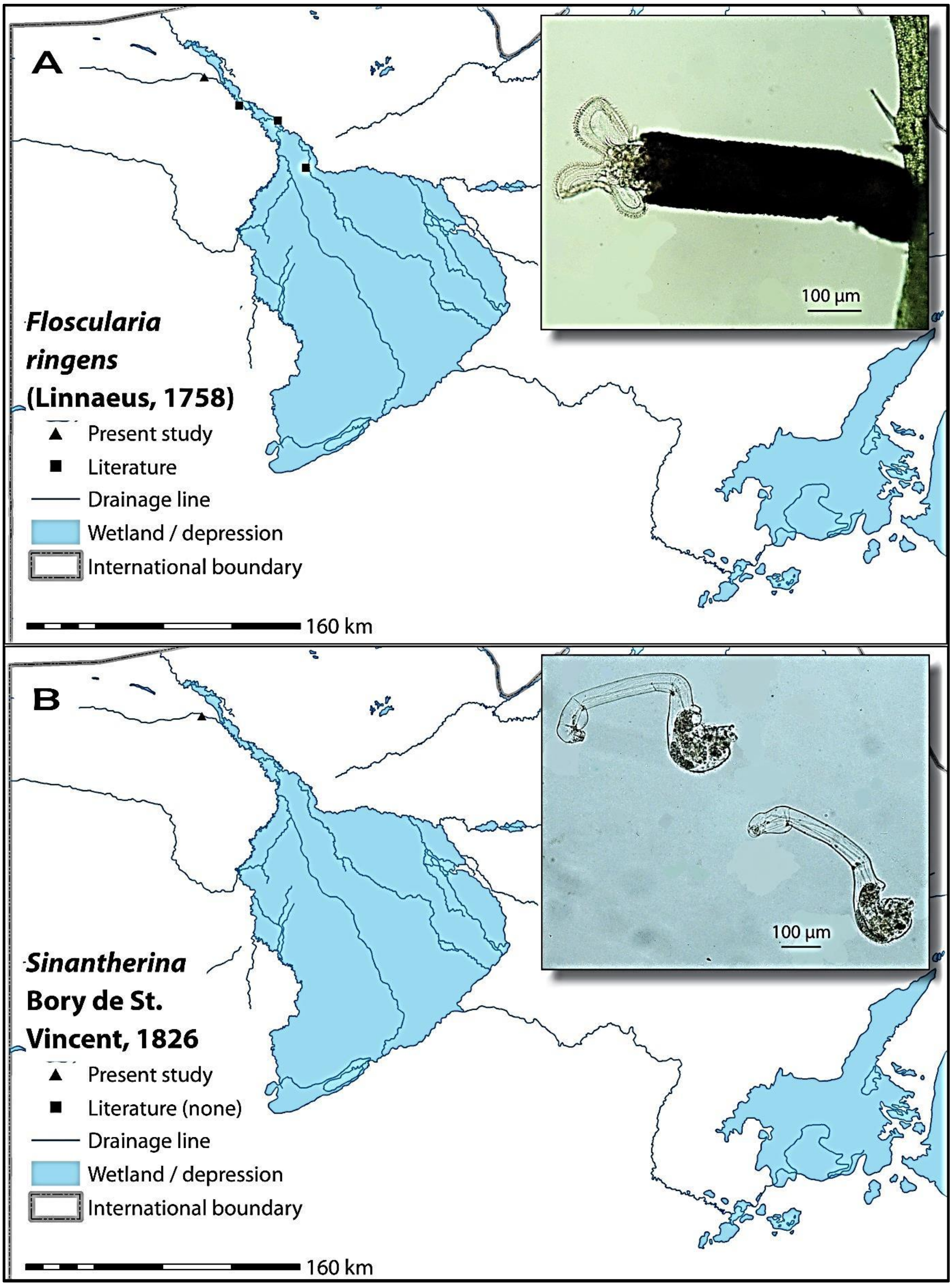

Figure 5.18: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A:** *Floscularia ringens* (Linnaeus, 1758) and **B**: *Sinantherina* Bory de St. Vincent, 1826 sp. throughout the Okavango Delta and its associated basins, Botswana.

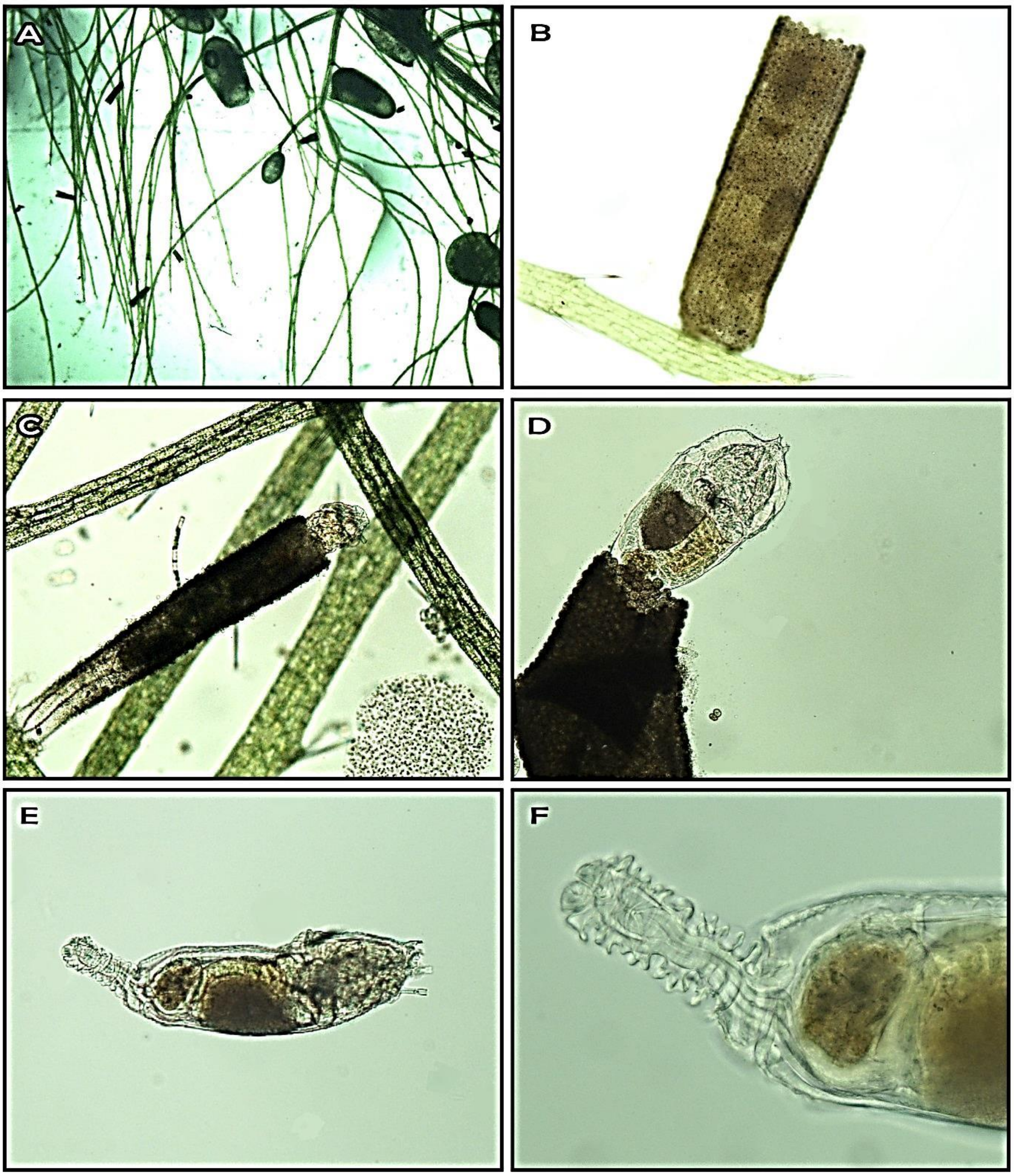

Figure 5.19: Photomicrographs of the monogonont rotifer *Floscularia ringens* (Linnaeus, 1758) collected from the Nxamasere Floodplain, Okavango Delta Panhandle, in July 2013. **A**: A colony of the sessile *F. ringens* attached to aquatic flora. **B**, **C** & **D**: Individuals of *F. ringens* use detritus to form pellets which they arrange like bricks into a small tube in which they settle. **E**: An individual specimen outside of its tube. **F**: The foot of *F. ringens*.

FAMILY HEXARTHRIDAE Bartos, 1959

Genus *Hexarthra* Schmarda, 1854 (Fig. 5.20A)

An unidentified species of the genus *Hexarthra*, most likely *Hexarthra mira* (Hudson, 1871), was sampled on only one occasion, in September 2012, from the Nxamasere Floodplain (NX03) (Fig. 5.20A). This is another example of a species that did not preserve well, as it was only identifiable from photomicrographs of live specimens and, therefore, could not be identified up to species level. *Hexarthra mira* has previously been identified from the Okavango Panhandle (Hart 1997), the lower Okavango Delta, the Thamalakane River and the upper Boteti River (Green 2003) (Fig. 5.20A).

Members of the genus *Hexarthra* are able to feed on suspended bacteria and detritus, hence their abundance may be an indication of mesotrophic conditions (Pereira *et al*. 2002). The Okavango Panhandle is oligotrophic with extremely low nutrient levels (West *et al.* 2015), which would explain why this genus was not more abundant and widespread. However, the pools in the Nxamasere Floodplain, where the *Hexarthra* species was present, have a higher nutrient level than the rest of the panhandle, due to evaporative concentration (West *et al.* 2015). This may explain why it successfully occurs there. The same conditions apply for the pools at Seronga where the genus was sampled by Hart (1997). It is unclear as to what the water levels, and hence evaporative concentration, was during Green's (2003) study when he sampled the genus from the lower delta and its outlets, but the presence of this genus may be an indication that nutrient levels were slightly elevated at the time.

FAMILY TESTUDINELLIDAE Harring, 1913

Genus *Pompholyx* Gosse, 1951 (Fig. 5.20B)

Pompholyx sulcata has only been found in a very localised area in the lower reaches of the Okavango Delta (in and around the Thamalakane River) on one occasion during the present study and once by Green (2003) (Fig. 5.20B). This species is never present in large numbers and is planktonic. It is generally a freshwater species, but may also be found in salt waters of low concentrations (Ruttner-Kolisko 1974).

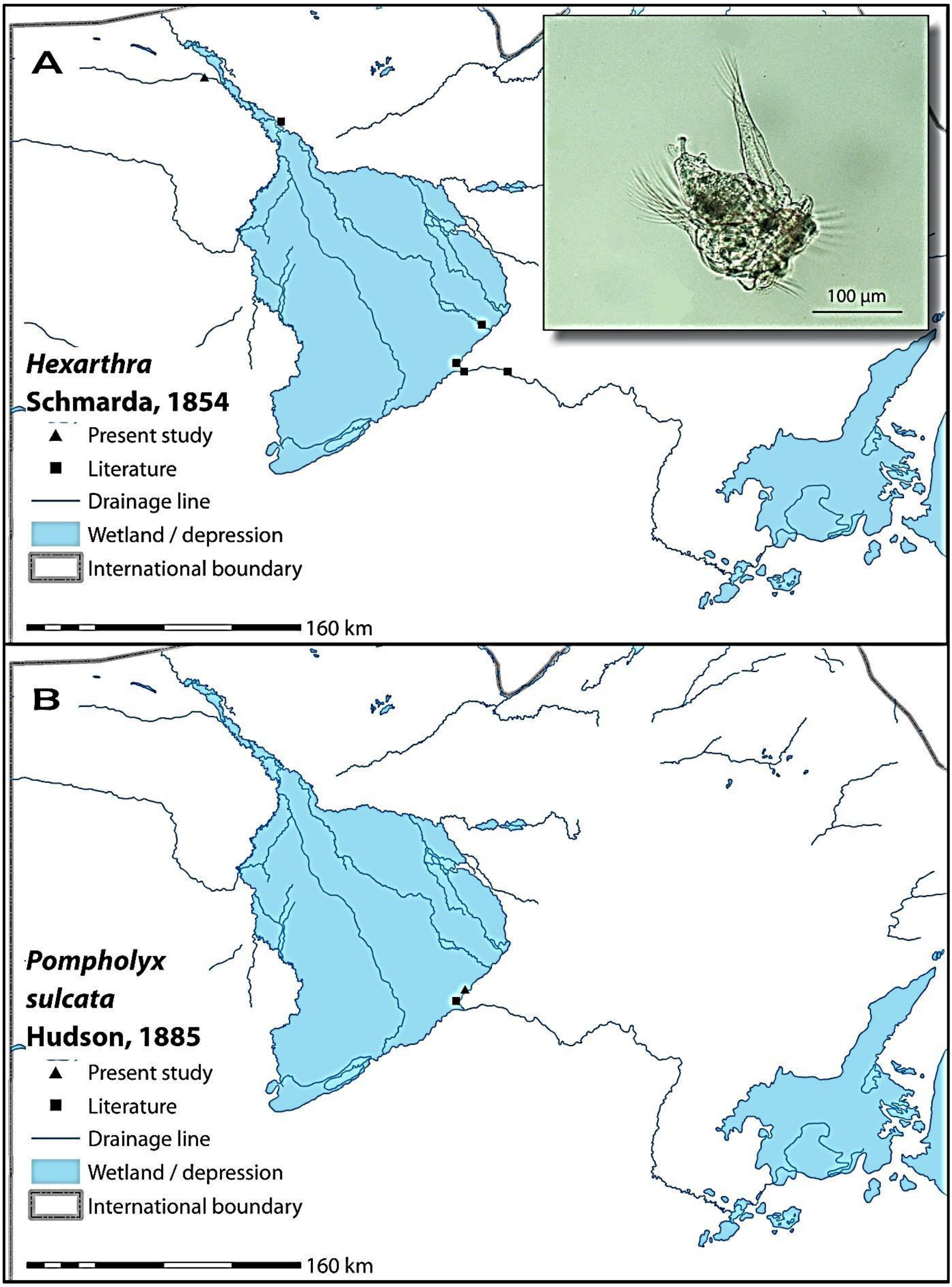

Figure 5.20: Geographic Information System (GIS) maps indicating the distribution of the rotifers **A:** *Hexarthra* Schmarda, 1854 sp. and **B**: *Pompholyx sulcata* Hudson, 1885 throughout the Okavango Delta and its associated basins, Botswana.

ORDER BDELLOIDEA

In the Okavango Delta and its associated basins, the order Bdelloidea was represented by a single species of the genus *Rotaria* and family Philodinidae. Species of Bdelloidea are able to inhabit a wide variety of environments, mainly due to two biological characteristics. The first is obligatory parthenogenesis by which to escape critical population density and the second is entering a dormant state, called anhydrobiosis, in order to resist desiccation (Ricci 1998) (see **Chapter 3**).

Ricci and Melone (2000) point out that although bdelloid rotifers play a key role in food webs, most studies recording freshwater micro-invertebrate assemblages disregard bdelloids or do not identify them up to species level. Hence, information on the occurrence of taxa is scarce and unsatisfactory. They (Ricci & Melone 2000) continue that the group is neglected due to the difficulty in identifying taxa. Most bdelloids can only be identified while alive, active, feeding and crawling, as some taxonomically important traits can only be observed while they are active. Furthermore, identification keys are few and not up to date (Ricci & Melone 2000). One and a half decades later, the shortage of up-to-date identification keys was clear during the present study. Fortunately, live observations were made and photomicrographs were taken of live specimens moving about which enabled the bdelloid species present in the system to be identified.

FAMILY PHILODINIDAE Ehrenberg, 1838

Genus *Rotaria* Scopoli, 1777 (Fig. 5.21)

Most species of the genus *Rotaria* live in water bodies, but a number can be found in soil as well as moss (Ricci & Melone 2000). *Rotaria neptunia* was sampled from the Okavango Panhandle (in the Ngarangi Floodplain) in July 2013. It was also reported from the upper reaches of the Okavango Delta Fan by Green (2003) (Fig. 5.21). Identification of this species was made possible by both live observations at a field laboratory almost immediately after collection, as well as the possession of photomicrographs of live specimens, which were taken in the field (Figs. 3.2 & 5.21).

Rotaria neptunia is an extremely tolerant, benthic rotifer which is able to survive in anoxic conditions for some time (Kansanen 1981). In fact, Kansanen (1981) stated that *R. neptunia* may become abundant in environments in which abiotic factors are too severe for most predators. This species was also present in the saline waters of the Nata River during the present study (see **Chapter 8**). The reason that this species was only encountered once in the Okavango and its associated basins may be because it is a benthic organism and not readily collected with a plankton net.

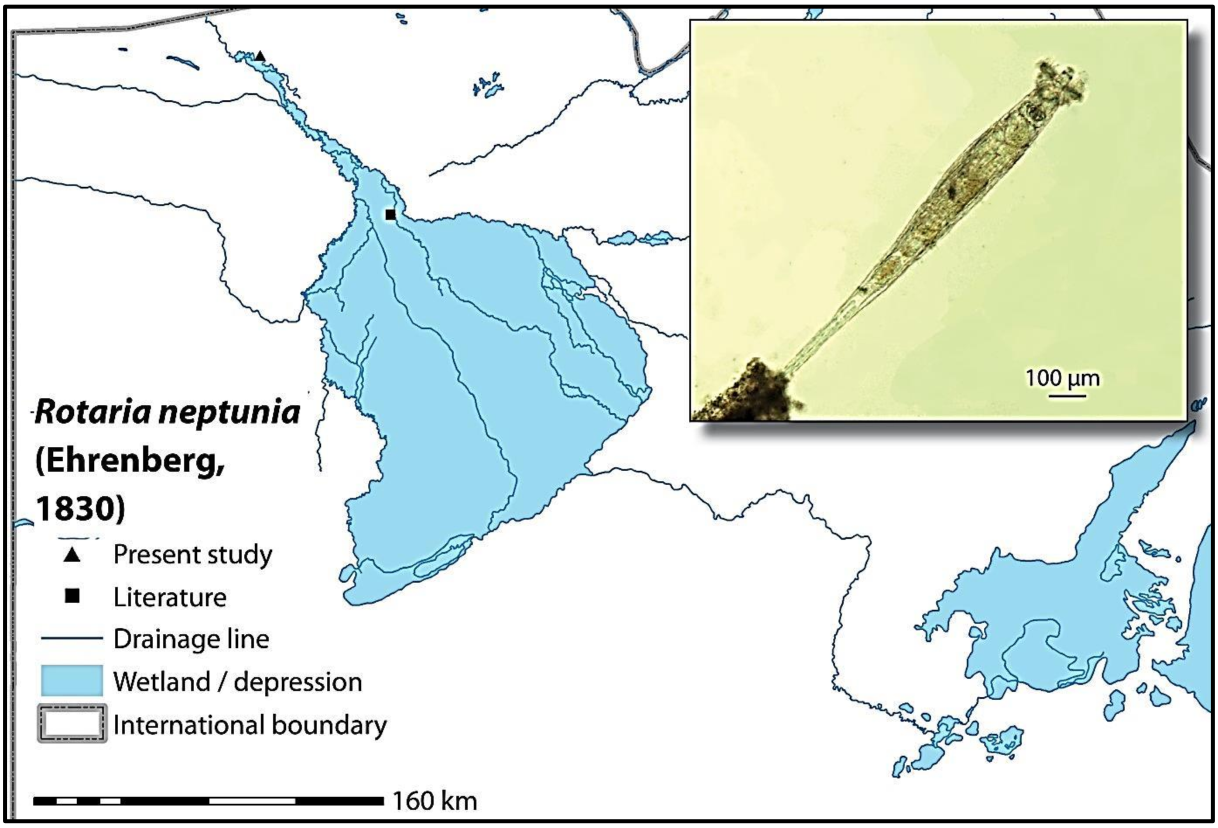

Figure 5.21: Geographic Information System (GIS) maps indicating the distribution of the rotifer *Rotaria neptunia* (Ehrenberg, 1830) throughout the Okavango Delta and its associated basins, Botswana.

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Chapter 6

TAXONOMIC ACCOUNT AND DISTRIBUTION OF CLADOCERA

INTRODUCTION

Cladocerans are critical components of freshwater food webs, particularly in stagnant water (Forró *et al*. 2008). Although research into the systematics, taxonomy and diversity of cladocerans has increased in certain geographical areas and decreased in others, Cladocera have always remained relatively poorly studied on the African continent (Van Damme *et al*. 2013). In northern Botswana, cladoceran records include those conducted by Cronberg *et al*. (1995), Hart (1997), Høberg *et al*. (2002), Lindholm (2002), Hart *et al*. (2003), Hart and Dumont (2005), Lindholm and Hessen (2007), Lindholm *et al*. (2007; 2009) and Siziba *et al*. (2011a; 2011b; 2013).

As mentioned in **Chapter 5**, Cronberg *et al.* (1995) conducted a hydrological study in the Kwando/Linyanti/Chobe System and included the presence of phytoplankton and zooplankton, while Hart (1997) compiled a limnological profile of the lower panhandle at Seronga based on 'a modest survey' conducted in 1986. Hart and Dumont (2005) wrote a research letter in which they report on the finding of a Holarctic taxon, *Lathonura* Lilljeborg, 1853 sp., from the Okavango Delta, based on a single specimen. This paper only makes mention of the one species and is therefore omitted from the discussion on the Cladocera of the Okavango Delta and its associated basin in the present study. Lindholm *et al*. (2007) conducted predation experiments on a cladoceran community of a floodplain within the Okavango and only included three species, namely *Daphnia laevis* Birge, 1878, *Ceriodaphnia reticulata* (Jurine, 1820) and *Scapholeberis kingi* Sars, 1888. During the course of a flooding period, Lindholm and Hessen (2007) studied plankton development and zooplankton species succession south of Chief's Island in the Okavango Delta Fan, but only mentioned two cladoceran species, namely *Daphnia laevis* and *Moina micrura* Kurz, 1874. Lindholm *et al*. (2009) conducted a study which aimed at recording the cladoceran species composition in the Okavango Delta. The study was conducted in a relatively large area south of Chief's Island in the Okavango Delta Fan only. Siziba *et al.* (2011a) identified micro-invertebrates, including cladocerans, collected from a localised area south of Chief's Island and Siziba *et al*. (2011b) aimed to determine the spatial variations of micro-invertebrates across the microhabitats of the Okavango Delta's temporary floodplains. The latter study did not include a species list and was conducted in the same area as that of Siziba *et al*. (2011a). Siziba *et al*. (2013) examined the community structure of small fishes and micro-crustaceans in flooded areas of the Okavango Delta Fan between Chief's Island and Maun. Figure 6.1 indicates the areas in which these studies were conducted, as well as the cladoceran sampling sites of the present study.

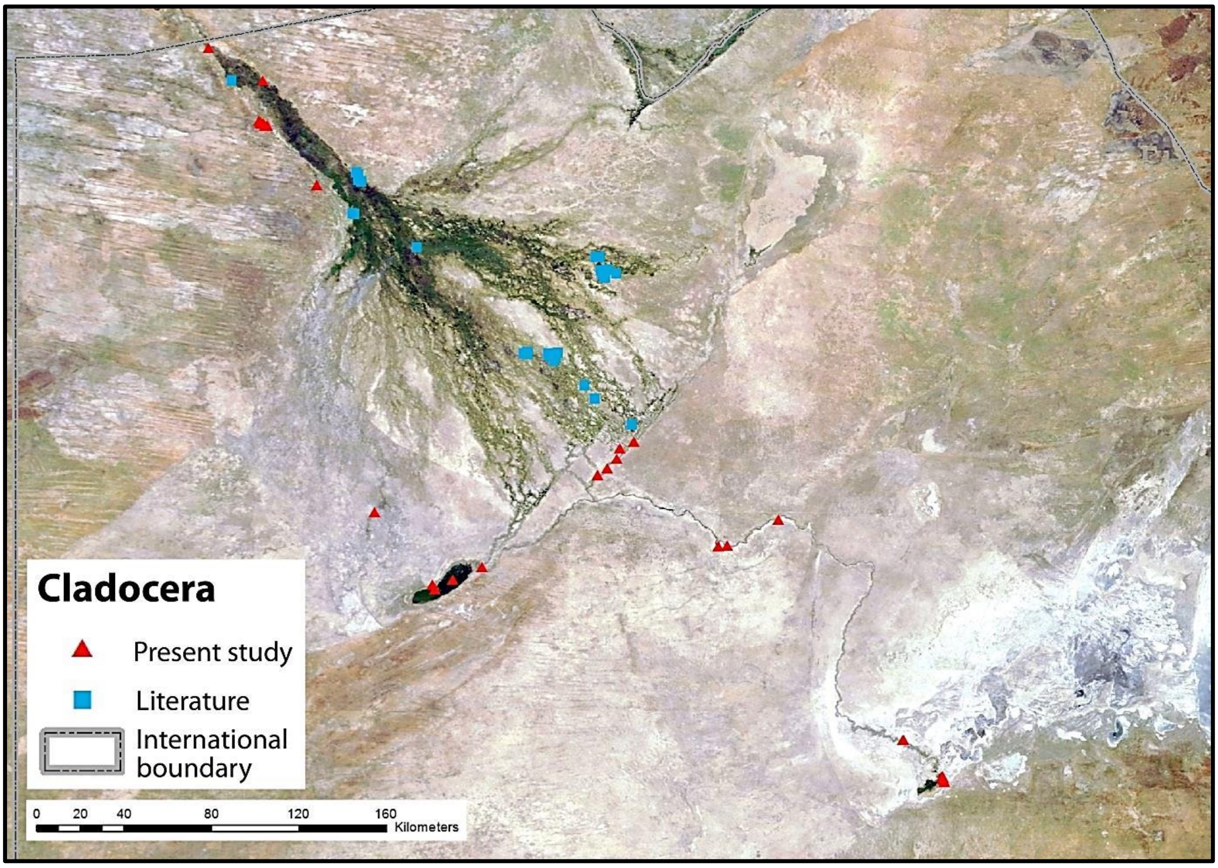

Figure 6.1: Geographic Information System (GIS) map indicating the sites within the Okavango Delta and its associated basins in northern Botswana where Cladocera samples were collected during the present study in 2011, 2012 and 2013 as well as where data was available for Cladocera from previous studies.

The aim of the present study was to determine the taxonomic composition of Cladocera from the Okavango Panhandle (which has been largely neglected in terms of limnological research), parts of the delta fan as well as the ephemeral basins in northern Botswana which are associated with the Okavango Delta. Previous studies on Cladocera have been conducted in the Okavango Panhandle and the Okavango Delta Fan (Fig. 6.1), but no attempt has been made to study the systematics of cladocerans from the water bodies south of the Okavango, namely the Thamalakane and upper Boteti Rivers. Furthermore, sampling of Cladocera from basins such as Lake Ngami, the lower Boteti River and Lake Xau have not been possible for 20 to 30 years due to continuing drought. The perfect opportunity to sample from these systems, which have already begun to dry up again, presented itself following the 2010 floods (see **Chapter 2**). This study also aimed at determining the distribution of Cladocera species, amongst others, across the Okavango Delta and its associated basins by combining data from previous studies (Cronberg *et al*. 1995; Hart 1997; Høberg *et al*. 2002; Lindholm 2002; Hart *et al*. 2003; Lindholm & Hessen 2007; Lindholm *et al.* 2007; 2009; Siziba *et al*. 2011a; 2011b; 2013) with that of the present study. In this chapter, the first records of Cladocera from the Thaoge Channel (western Okavango Delta Fan) (Fig. 2.7), the Thamalakane River, Lake Ngami, the Boteti River and Lake Xau (Figs. 2.4, 4.1, 4.2, 4.3 & 6.1) are provided.

RESULTS AND REMARKS

Chydoridae excluded, 45 cladoceran samples collected from 38 study sites in the Okavango Panhandle, Okavango Delta, Thamalakane River, Lake Ngami, Boteti River and Lake Xau revealed a total of 12 species which belong to nine genera and five families. Furthermore, a number of unidentified species and genera belonging to the Chydoridae were widely distributed and often encountered. Hence, there were representatives of six families and more than the above-mentioned number of species and genera. All Cladocera taxa were of the order Anomopoda under the class Branchiopoda and are listed in Table 6.1.

The family Chydoridae was the most diverse of all the families of Cladocera in the Okavango Delta and its associated basins. A number of different taxa were encountered throughout the region, but were left unidentified for the purposes of this document. This is because our knowledge on the cladoceran fauna, and especially the Chydoridae, of southern Africa is hardly satisfactory (Sinev 2006; [2]Kořínek 2014, Personal communication).

The genus with the most representatives was *Ceriodaphnia* Dana, 1853 (comprising three species), followed by *Simocephalus* Schoedler, 1858 (comprising two species).

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[2] Prof. Vladimír Kořínek: Professor Emeritus, Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic.

The genera *Bosmina* Baird, 1845, *Daphnia* Müller, 1785, *Scapholeberis* Schoedler, 1858, *Echinisca* Liévin, 1848, *Ilyocryptus* Sars, 1861, *Macrothrix* Baird, 1843 and *Moina* Baird, 1850 were represented by a single species, respectively (Table 6.1).

Species diversity at the various study sites ranged from zero at sites in the Nxamasere Floodplain and Maun05 (lower reaches of the Okavango Delta Fan) to eight species at Makalamabedi02 (where no chydorids were present) in the Boteti River. Other sites with a relatively high cladoceran species diversity were Thaoge Tsau in the Thaoge Channel (Okavango Delta Fan) with seven species and NX01, NX11 and NX15 (Nxamasere Floodplain) with six species each.

Cladoceran species were generally widely distributed except for *Ilyocryptus sordidus* (Liévin, 1848) which was only collected in the Nxamasere Floodplain in the upper panhandle and in the Boteti River (Makalamabedi 02). Table 6.2 lists the Cladocera species sampled in the Okavango Delta and its associated basins in order of distribution, from highest to lowest frequency, and provides the study sites at which each species was found.

Table 6.1: Anomopoda (Cladocera) taxa recorded in northern Botswana in 2011, 2012 and 2013.

PHYLUM ARTHROPODA	
CLASS BRANCHIOPODA	
Order Anomopoda	
Family Bosminidae Baird, 184	**Family Daphniidae** *(continued)*
Bosmina longirostris (Müller, 1776)	*Simocephalus serrulatus* (Koch, 1841)
Family Chydoridae Stebbing, 1902	*Simocephalus vetulus* (Müller, 1776)
Species unidentified*	**Family Macrothricidae Norman & Brady, 1867**
Family Daphniidae Straus, 1820	*Echinisca* Liévin, 1848 sp.
Ceriodaphnia quadrangula (Müller, 1785)	*Ilyocryptus sordidus* (Liévin, 1848)
Ceriodaphnia reticulata (Jurine, 1820)	*Macrothrix propinqua* Sars, 1909
Ceriodaphnia rigaudi Richard, 1894	**Family Moinidae Goulden, 1968**
Daphnia laevis Birge, 1878	*Moina micrura* Kurz, 1874
Scapholeberis kingi Sars, 1888	

* The Chydoridae spp. are included in the species diversity lists as a single taxon.

Table 6.2: Distribution of Anomopoda (Cladocera) taxa collected in northern Botswana in 2011, 2012 and 2013. Taxa are presented from highest to lowest frequency. Study sites within the various water bodies are presented in a colour code as follows: 1. Okavango Panhandle, 2. Okavango Delta, 3. Thamalakane River, 4. Lake Ngami, 5. Boteti River and 6. Lake Xau. 'N' indicates the number of water bodies in which the species were present.

CLADOCERA TAXA	STUDY SITES	N
Chydoridae Stebbing, 1902 spp.	Ngarangi Floodplain, NX01'13, NX02, NX06, NX09, NX11, Thaoge Tsau, Maun03'12, Maun02, Maun04'12, MaunTJL, Nhabe, Makalamabedi01, Makalamabedi02, Motopi, Xhumo Bridge'11, LX03. =16	6
Ceriodaphnia quadrangula (Müller, 1785)	Mohembo Pool, NX01'13, NX03'12, NX05 NX07, NX09, NX11, NX15, Ikoga, Thaoge Tsau, MaunTJL LN01'13, LN03, Makalamabedi02, LX03. =15	6
Ceriodaphnia rigaudi Richard, 1894	NX02, NX05, NX07, NX12, NX15, Ikoga, Thaoge Tsau, Maun04'11, LN03, Makalamabedi02, LX01. =11	6
Simocephalus vetulus (Müller, 1776)	NX06, NX09, Thaoge Tsau, Maun03'11, LN01'11, LN01'12, LN02, Nhabe, Makalamabedi02, Motopi, Xhumo Bridge'11, Xhumo Bridge'12, LX01, LX02, LX03, LX04, LX05. =15	5
Macrothrix propinqua Sars, 1909	NX07, NX11, NX12, Maun03'12, Thaoge Tsau, LN01'12, LN02, LN01'13, Makalamabedi02, Motopi, Xhumo Bridge'11, LX03, LX05. =12	5
Moina micrura Kurz, 1874	Mohembo Pool, NX03'12, NX15, Ikoga, Thaoge Tsau, LN01'11, LN01'12, LN01'13, N02, LN03, Makalamabedi01, LX04. =10	5
Scapholeberis kingi Sars, 1888	NX01'13, Maun04'12, LN01'12, LN02, Makalamabedi02, Xhumo Bridge'12. =6	4
Ceriodaphnia reticulata (Jurine, 1820)	Mohembo Pool, NX05, NX07, NX11, NX15, MaunTJL, LX01, LX02, LX03, LX04. =10	3
Bosmina longirostris (Müller, 1776)	Mohembo Pool, NX09, NX15, Ikoga, Maun02, MaunTJL, LN01'12, LN01'13, N02, LN03. =9	3
Daphnia laevis Birge, 1878	NX05, NX12, NX15, Ikoga, Thaoge Tsau, LN01'11. =6	3
Simocephalus serrulatus (Koch, 1841)	NX01'13, NX02, Maun02, MaunTJL, Makalamabedi02.=5	3

Table 6.2 (Cont.): Distribution of Anomopoda (Cladocera) taxa collected in northern Botswana in 2011, 2012 and 2013. Taxa are presented from highest to lowest frequency. Study sites within the various water bodies are presented in a colour code as follows: 1. Okavango Panhandle, 2. Okavango Delta, 3. Thamalakane River, 4. Lake Ngami, 5. Boteti River and 6. Lake Xau. 'N' indicates the number of water bodies in which the species were present.

CLADOCERA TAXA	STUDY SITES	N
Echinisca Liévin, 1848 sp.	NX01'13, NX02, NX11, Maun03'11, Makalamabedi01. =5	3
Ilyocryptus sordidus (Liévin, 1848)	NX01'13, NX02, Makalamabedi02 . =3	2

ORDER ANOMOPODA

Anomopoda is the most diverse order of Cladocera which is represented by 11 families worldwide. Only seven of these families have been recorded from the Afrotropical region (see **Chapter 3**) (Forró *et al.* 2008) and five of the seven were present in the Okavango Delta and its associated basins during the present study.

FAMILY BOSMINIDAE Baird, 1845

Two genera and three species of Bosminidae have been recorded from the Afrotropics (Forró *et al.* 2008), but only one genus and one species occur in southern Africa (Seaman *et al*. 1999).

Genus *Bosmina* Baird, 1845 (Fig. 6.2A)

Bosmina longirostris (Müller, 1776) was frequently encountered across the Okavango Panhandle at NX09, NX15 and Ikoga in 2011 and at Mohembo Pool in 2013. In the Thamalakane River, *B. longirostris* was present at Maun02 in 2011 and at MaunTJL in 2012. In 2012 it was present in high densities throughout Lake Ngami (LN01, LN02 & LN03) and was also sampled from the lake (LN01) in 2013. Although *B. longirostris* was not sampled from the outskirts of the Okavango Delta Fan during the present study, previous studies (Cronberg *et al*. 1995; Høberg *et al.* 2002; Lindholm 2002; Hart *et al.* 2003; Lindholm *et al.* 2009; Siziba *et al*. 2011a; 2011b;

2013) reported the species from the area around Chief's Island and the eastern parts of the delta. It was also reported from the panhandle by Hart (1997) and Hart *et al.* (2003). *Bosmina longirostris* was not sampled from the Boteti River or Lake Xau, south of the Thamalakane (Fig. 6.2A).

FAMILY CHYDORIDAE Stebbing, 1902 (Fig. 6.2B)

The Chydoridae are littoral dwellers and although some are efficient swimmers, they mainly crawl or scramble over substrate (Fryer 1968). It is the most taxonomically confusing of the southern African cladoceran families. More species exist than have been described and species formerly thought to be a single taxon, as they are morphologically similar, are in fact separate species from different geographical regions (Seaman *et al*. 1999). Much doubt remains about the identity of species and Seaman *et al*. (1999) suggested that until the taxonomy of local species is reviewed in detail, identification should be considered uncertain. In order not to add to the confusion of chydorid taxonomy, species diversity and distribution in southern Africa, species were left unidentified for the purposes of the present study. Reference material, however, remains in the collection of the Aquatic Ecology Research Group, University of the Free State, for future detailed examination.

A number of chydorid taxa were present throughout the Okavango Delta and its associated basins in 2011, 2012 and 2013. Study sites at which members of the Chydoridae were found are listed in Table 6.2 and indicated in Figure 6.2B. Chydoridae species were not present in Lake Ngami, but were collected at the inlet to the lake (Nhabe). It is clear that the Chydoridae are very successful organisms in the Okavango and its associated basins, which points out the need for an in-depth study into this group of organisms.

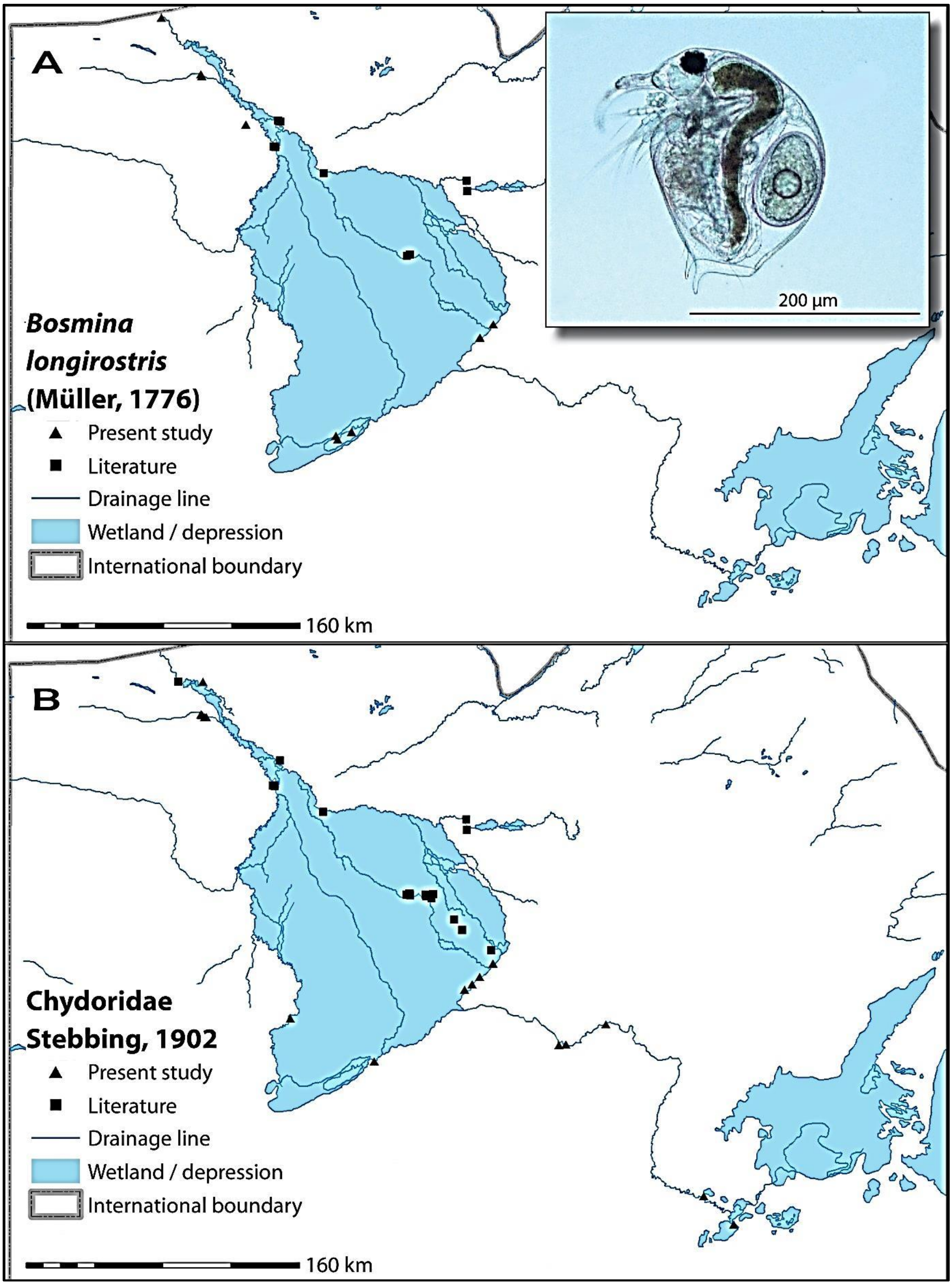

Figure 6.2: Geographic Information System (GIS) maps indicating the distribution of the cladocerans **A**: *Bosmina longirostris* (Müller, 1776) and **B**: Chydoridae Stebbing, 1902 spp. throughout the Okavango Delta and its associated basins, Botswana.

FAMILY DAPHNIIDAE Straus, 1820

Five genera belonging to the family Daphniidae occur in the Afrotropical region (Forró *et al.* 2008) and more specifically in southern Africa (Seaman *et al*. 1999). This was the most diverse family of Cladocera in the Okavango Delta and its associated basins with four genera (*Ceriodaphnia*, *Daphnia*, *Scapholeberis* and *Simocephalus*) and seven species present.

The family Daphniidae contains the most well-known cladocerans (Seaman *et al*. 1999) although some authors (Seaman *et al*. 1999; Van Damme *et al*. 2013) believe that the number of endemic taxa described from southern Africa is likely to increase with thorough studies.

Genus *Ceriodaphnia* Dana, 1853 (Figs. 6.3, 6.4A & 6.4B)

Species of the genus *Ceriodaphnia* are found in a variety of habitats (Seaman *et al*. 1999) and the genus was the most diverse in the Okavango Delta and its associated basins. It was represented by three widely distributed species, namely *Ceriodaphnia quadrangula* (Müller, 1785), *C. reticulata* (Jurine, 1820) and *C. rigaudi* Richard, 1894.

Ceriodaphnia quadrangula was present in all water bodies (Okavango Panhandle, Okavango Delta Fan, the Thamalakane River, Lake Ngami, the Boteti River and Lake Xau) at certain times during the study (Table 6.2) (Fig. 6.3). In the panhandle, *C. quadrangula* was sampled at NX05, NX09, NX15 and Ikoga in 2011, NX03 and Mohembo Pool in 2012 and NX01, NX07 and NX11 in 2013. In the outskirts of the Okavango Delta Fan it was found at Thaoge Tsau in 2012 and in the Thamalakane River the species was sampled at MaunTJL in 2012. *Ceriodaphnia quadrangular* was present in Lake Ngami in 2012 (LN03) and in 2013 (LN01). In 2011 this species was present in Lake Xau (LX03), but not in the Boteti River and then in 2012 it was present in the Boteti (Makalamabedi02), but not in Lake Xau (Fig. 6.3). Previous studies recorded *C. quadrangula* in the lower panhandle (Hart 1997) and in the Okavango Delta Fan (Høberg *et al.* 2002; Siziba *et al*. 2011a) (Fig. 6.3).

Ceriodaphnia reticulata was the least widely distributed of the three *Ceriodaphnia* species and was sampled in the Okavango Panhandle, the Thamalakane River and Lake Xau. It was not found in the outskirts of the Okavango Delta Fan, Lake Ngami or the Boteti River (Fig. 6.4A). In the panhandle, *C. reticulata* was present at NX05 and NX15 in 2011, Mohembo Pool in 2012 and NX07 and NX11 in 2013. It was sampled on one occasion from the Thamalakane River (MaunTJL) in 2012 and was present in Lake Xau in both 2011 (LX01, LX02 and LX03) and 2012 (LX04). *Ceriodaphnia reticulata* was not recorded from the Okavango Panhandle during previous studies but was found in the Okavango Delta Fan (Lindholm *et al.* 2007; 2009) (Fig. 6.4A).

Ceriodaphnia rigaudi was present in all water bodies throughout the study area. In the panhandle it was sampled at NX05, NX12, NX15, Ikoga (in 2011), NX02 (in 2012) and NX07 (in 2013). The species was sampled at Thaoge Tsau (2012) and Maun04 (2011) in the outskirts of the delta fan and in the Thamalakane River, respectively. *Ceriodaphnia rigaudi* was not present in Lake Ngami in 2011 or 2013, but in 2012 it was sampled from the centre of the Lake at LN03. In the Boteti River the species was present at Makalamabedi02 in 2012 and in Lake Xau it was found at LX01 in 2011. *Ceriodaphnia rigaudi* was reported only once by a previous author (Hart 1997) in the lower panhandle (Fig. 6.4B).

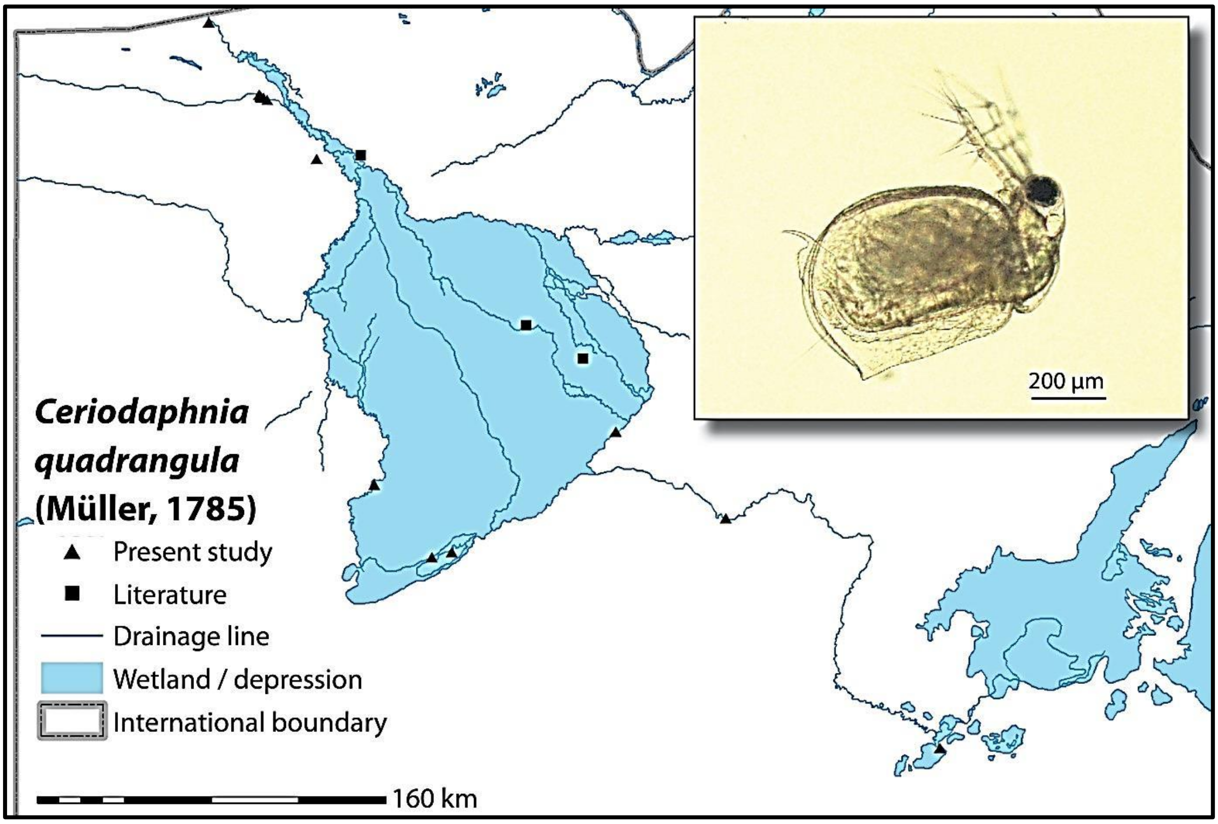

Figure 6.3: Geographic Information System (GIS) map indicating the distribution of the cladoceran *Ceriodaphnia quadrangula* (Müller, 1785) throughout the Okavango Delta and its associated basins, Botswana.

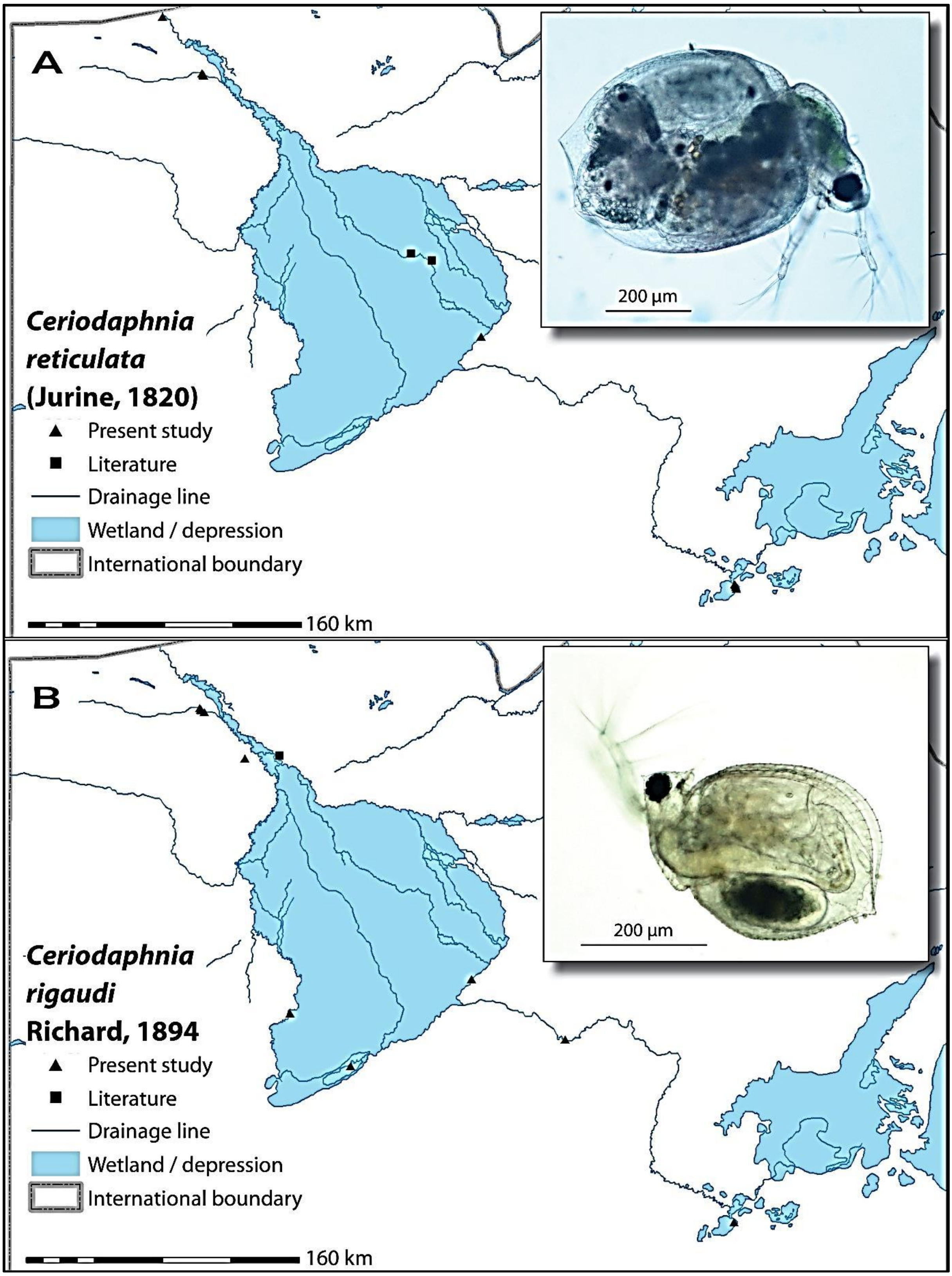

Figure 6.4: Geographic Information System (GIS) maps indicating the distribution of the cladocerans **A**: *Ceriodaphnia reticulata* (Jurine, 1820) and **B**: *Ceriodaphnia rigaudi* Richard, 1894 throughout the Okavango Delta and its associated basins, Botswana.

Genus *Daphnia* Müller, 1785 (Fig. 6.5A)

The majority of *Daphnia* species are limnetic (Seaman *et al*. 1999) and live in the plankton (Siziba *et al*. 2011b). Only one species of these large-bodied cladocerans has been collected from the waterways of northern Botswana, namely *Daphnia laevis* Birge, 1878. In August 2011 it was widespread throughout the panhandle (NX05, NX12, NX15 and Ikoga) and present in Lake Ngami (LN01) as well. In August 2012, however, it was only collected in the Thaoge Channel (Thaoge Tsau) and was not at all collected in 2013. Furthermore, *D. laevis* was not present in and around Maun, in the Boteti River or in Lake Xau during the present study (Fig. 6.5A). Siziba *et al*. (2011b) also reported that numbers of this species were low in the Okavango Delta Fan during their study. This may be due to high predation pressure in the limnetic zone by the surge of juvenile fish and small fish species during the unusually high flood.

Daphnia laevis has previously been recorded from the Okavango Delta Fan (Cronberg *et al*. 1995; Høberg *et al.* 2002; Lindholm 2002; Lindholm & Hessen 2007; Lindholm *et al.* 2007; 2009; Siziba *et al*. 2011a; 2011b; 2013) as well as the southern end of the panhandle (Hart 1997) (Fig. 6.5A).

Genus *Scapholeberis* Schoedler, 1858 (Fig. 6.5B)

Representatives of the genus *Scapholeberis*, like *Ceriodaphnia*, live in a variety of habitats (Seaman *et al*. 1999). This genus was represented by *Scapholeberis kingi* Sars, 1888 only, which seems to be a cosmopolitan species (Murugan & Sivaramakrishnan 1976). In their laboratory studies on the life-cycle of *S. kingi*, Murugan & Sivaramakrishnan (1976) found that individuals of this species can produce up to 239 eggs during a life span of about 20.56 days. This egg production, they stated, is higher than that of *Moina micrura* Kurz, 1874 and other species of *Daphnia*, *Ceriodaphnia* and *Simocephalus* for example.

In the Okavango Delta and its associated basins, *S. kingi* was not sampled at all during 2011, but in August 2012 it was sampled from the Thamalakane River (Maun04), Lake Ngami (LN01 and LN02) and the Boteti River (Makalamabedi02 and Xhumo Bridge). In July 2013 *S. kingi* was collected in the Nxamasere Floodplain

(NX01) in the panhandle for the first time during the study (Fig. 6.5B). This species has also been collected from a number of temporary pans in Mpumalanga, South Africa (Riato *et al*. 2014), suggesting that it is adapted to survive in temporary environments.

Despite being present in the Okavango Panhandle, the Thamalakane River, Lake Ngami and the Boteti River at different times during the present study, *S. kingi* was only sampled on one occasion by previous authors (Lindholm *et al.* 2007) in the Okavango Delta Fan (Fig. 6.5B).

Genus *Simocephalus* Schoedler, 1858 (Figs. 6.6A & 6.6B)

Species of the genus *Simocephalus* are freshwater cladocerans that may be found amongst aquatic vegetation in the littoral zones of water bodies (Orlova-Bienkowskaja 1998; Seaman *et al*. 1999). They have a world-wide distribution and have been known since the mid-eighteenth century, yet their taxonomy is still to be adequately clarified (Orlova-Bienkowskaja 1998). Two species of the genus *Simocephalus* were sampled in the Okavango Delta and its associated basins during the present study, namely *Simocephalus serrulatus* (Koch, 1841) and *Simocephalus vetulus* (Müller, 1776).

Simocephalus serrulatus was the least widely distributed of the two species. In August 2011 it was found in the Thamalakane River (Maun02) only, while in August 2012 it was present in the panhandle (NX02), the Thamalakane River (MaunTJL) and the Boteti River (Makalamabedi02). During the July 2013 survey it was only collected from the Nxamasere Floodplain (NX01) in the panhandle. Previous studies (Hart *et al.* 2003; Lindholm *et al.* 2009; Siziba *et al*. 2011a; 2013) have recorded this species from a number of locations within the eastern delta fan (Fig. 6.6A). *Simocephalus serrulatus* has a world-wide distribution and has been recorded from Europe, Asia, Africa, North America, South America and Australia (Orlova-Bienkowskaja 1998).

The most common species of the genus *Simocephalus* was *S. vetulus*. This species was collected from the panhandle (NX09 in 2011 and NX06 and NX11 in 2013), the outer delta fan (Maun03 in 2011 and Thaoge Tsau in 2012), Lake Ngami (LN01 and Nhabe in 2011, LN01 and LN02 in 2012 and LN01 in 2013), the Boteti River (Xhumo Bridge in 2011 and Makalamabedi02, Motopi and Xhumo Bridge in 2012) and Lake Xau (LX01, LX02 and LX03 IN 2011 and LX04 and LX05 in 2012) (Fig. 6.6B). Interestingly, in 2012, *Simocephalus vetulus* was the most dominant cladoceran species by far along the Boteti River and Lake Xau. The Thamalakane River was the only water body in which it was not found during the present study. During previous studies (Høberg *et al.* 2002; Lindholm 2002; Siziba *et al*. 2011b), *S. vetulus* was sampled in the central delta fan (Fig. 6.6B). In her revision of the genus *Simocephalus*, Orlova-Bienkowskaja (1998) stated that *S. vetulus* was previously assumed to be cosmopolitan, but that investigations showed that this species only occurs in Europe and North Africa and that it is replaced by other closely related species elsewhere. Apart from the present study and previous studies (Høberg *et al.* 2002; Lindholm 2002; Siziba *et al*. 2011b) reporting it from the Okavango Delta and its associated basin in Botswana, it has also been identified from the Cuvelai wetlands in northern Namibia (Clarke & Rayner 1999) and seasonal pools and pans in South Africa (Vanschoenwinkel *et al*. 2009; Riato *et al*. 2014). Hence it is not only present in North Africa, but is widespread in the temporary waters of southern Africa as well.

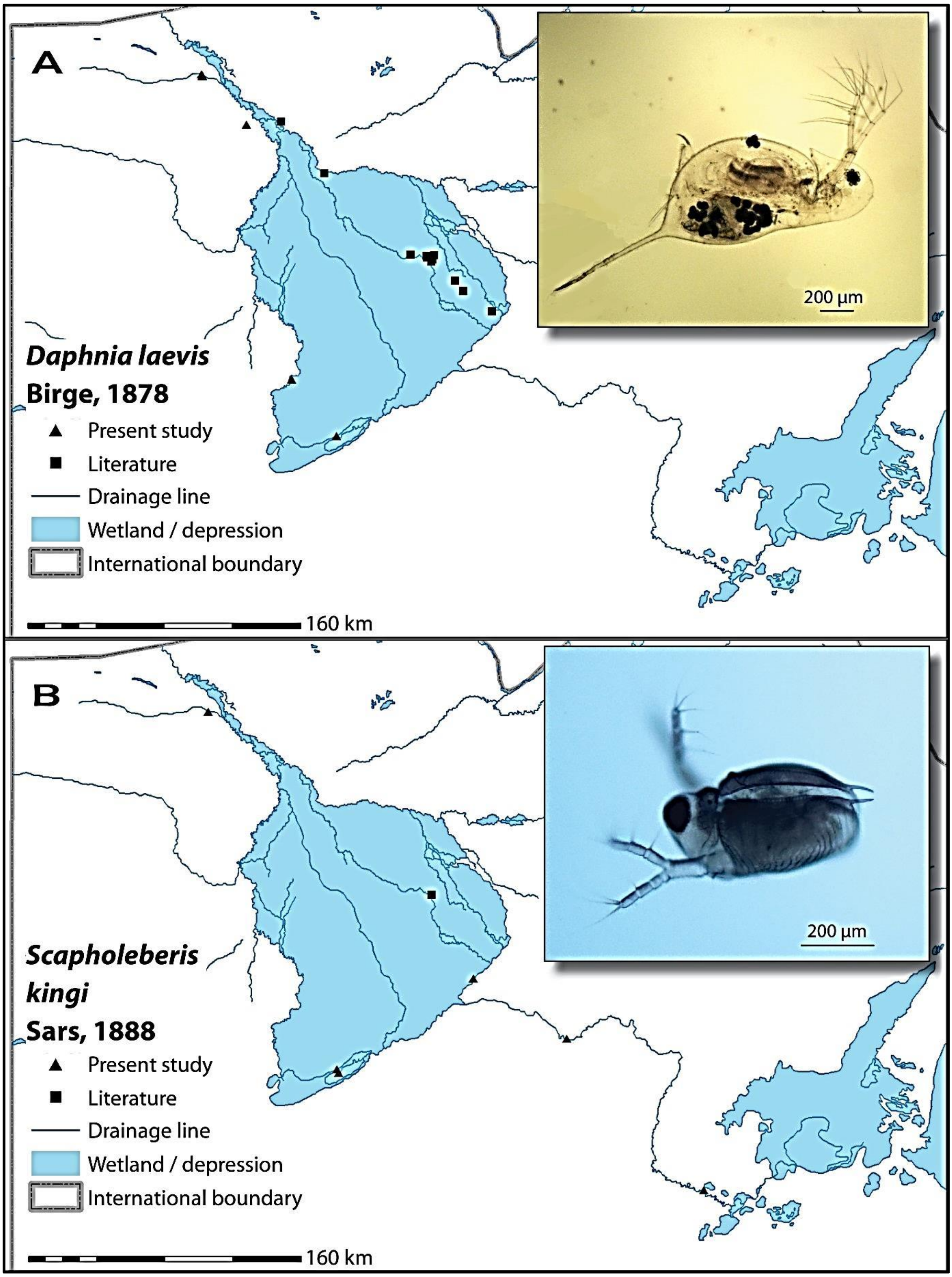

Figure 6.5: Geographic Information System (GIS) maps indicating the distribution of the cladocerans **A**: *Daphnia laevis* Birge, 1878 and **B**: *Scapholeberis kingi* Sars, 1888 throughout the Okavango Delta and its associated basins, Botswana.

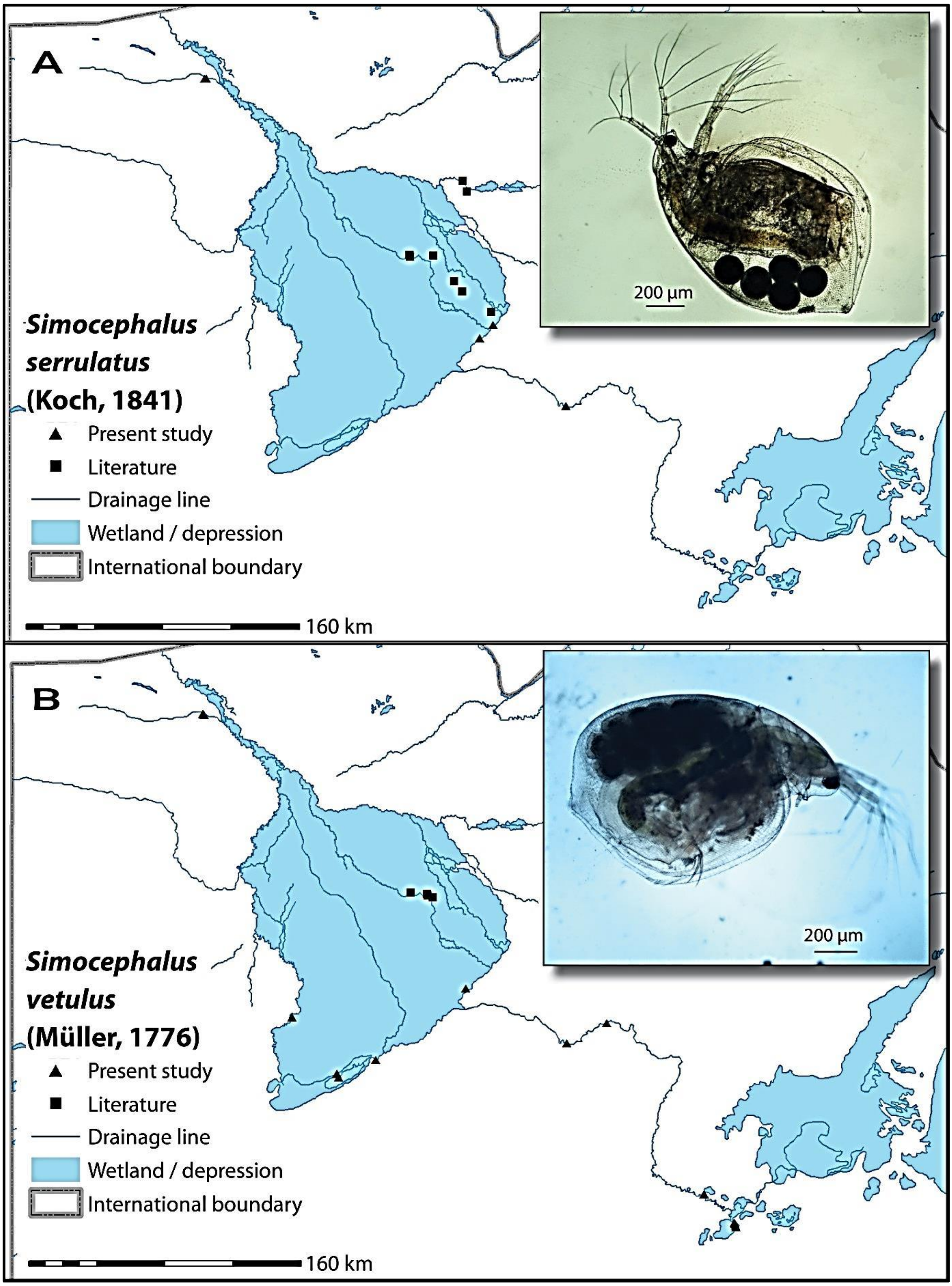

Figure 6.6: Geographic Information System (GIS) maps indicating the distribution of the cladocerans **A**: *Simocephalus serrulatus* (Koch, 1841) and **B**: *Simocephalus vetulus* (Müller, 1776) throughout the Okavango Delta and its associated basins, Botswana.

FAMILY MACROTHRICIDAE Norman & Brady, 1867

Five genera and 12 species of the family Macrothricidae are known from the Afrotropics (Forró *et al.* 2008), while three genera and five species are found in southern Africa (Seaman *et al*. 1999). All three these genera (*Echinisca, Ilyocryptus* and *Macrothrix*) and three of the five species were present in the Okavango Delta and its associated basins. Members of the Macrothricidae are generally found in the vegetated littoral zones close to the bottom of water bodies (Seaman *et al*. 1999).

Genus *Echinisca* Liévin, 1848 (Fig. 6.7A)

Only one species of *Echinisca* occurs in southern Africa and its species name is unclear (Seaman *et al*. 1999). This species (as illustrated by Seaman *et al*. 1999) was present in the Okavango Panhandle in August 2012 (NX02) and July 2013 (NX01 and NX11). In August 2011 it was found in the southern extremity of the Okavango Delta Fan (Maun03) and in the Boteti River (Makalamabedi01). Only a few specimens of this species were present in samples. A previous study (Hart *et al.* 2003) recorded *Echinisca* from the centre of the Okavango Delta Fan and the southern end of the panhandle (Fig. 6.7A).

Genus *Ilyocryptus* Sars, 1861 (Fig. 6.7B)

One of the two *Ilyocryptus* species which occur in southern Africa was collected in northern Botswana, namely *Ilyocryptus sordidus* (Liévin, 1848). This species is cosmopolitan (Seaman *et al*. 1999), but very cryptic and was collected as a hand-full of individuals in the panhandle (NX02) and the Boteti River (Makalamabedi02) in 2012 and again in the panhandle (NX01) in 2013. It was only found on one previous occasion from the Okavango Delta by Lindholm *et al.* (2009) (Fig. 6.7B).

Genus *Macrothrix* Baird, 1843 (Fig. 6.8A)

One of the two southern African *Macrothrix* species, *Macrothrix propinqua* Sars, 1909, was collected from all the water bodies in the study area, except the Thamalakane River. In August 2011 it was found in the panhandle (NX12), the Boteti River (Xhumo Bridge) and Lake Xau (LX03). The next year, in August 2012, *M. propinqua* was not present in the panhandle, but was sampled from the outer reaches of the delta fan (Maun03 and Thaoge Tsau), Lake Ngami (LN01 and LN02), the Boteti River (Makalamabedi02 and Motopi) and Lake Xau (LX05). *Macrothrix propinqua* was present in the panhandle (NX07 and NX11) and Lake Ngami (LN01) in July 2013 (Fig. 6.8A). This is the first record of *M. propinqua* in the Okavango Delta and its associated basins as it was not recorded from the area by previous authors. It has, however, been recorded from the Cuvelai Wetlands in Namibia (Clarke & Rayner 1999).

FAMILY MOINIDAE Goulden, 1968

Two genera of the family Moinidae (*Moina* and *Moinodaphnia*) are recognised worldwide and although both occur in the Afrotropics (Seaman *et al*. 1999; Forró *et al.* 2008), only *Moina* is found in southern Africa (Seaman *et al*. 1999). Four species are known from the region (Seaman *et al*. 1999), but only one was recorded in the study area (excluding the Nata River). *Moina* are mostly well adapted for survival in ephemeral pools and saline water bodies (Seaman *et al*. 1999).

Genus *Moina* Baird, 1850 (Fig. 6.8B)

Moina micrura was widely distributed throughout the region and the only water body it was not present in was the Thamalakane River. This species was found in Lake Ngami (LN01 in 2011 and 2013 and LN01, LN02 and LN03 in 2012) during all three sampling trips. In addition to this it was present in the panhandle (NX15 and Ikoga) and the Boteti River (Makalamabedi01) in 2011 and the panhandle (NX03 and Mohembo Pool), the Thaoge Channel (Thaoge Tsau) and Lake Xau (LX04) in 2012 (Fig. 6.8B). During previous studies it has been sampled from the eastern part of the Okavango Delta Fan (Høberg *et al.* 2002; Lindholm 2002; Lindholm & Hessen 2007; Lindholm *et al.* 2009; Siziba *et al*. 2011a; 2011b; 2013) (Fig. 6.8B). *Moina micrura* is commonly found in the natural and man-made lakes of Africa (Green 1971; Dumont *et al*. 1981; Hart 1985; Jarvis *et al.* 1987) and is also often encountered in the inland salt waters of southern Africa (Seaman *et al.* 1991).

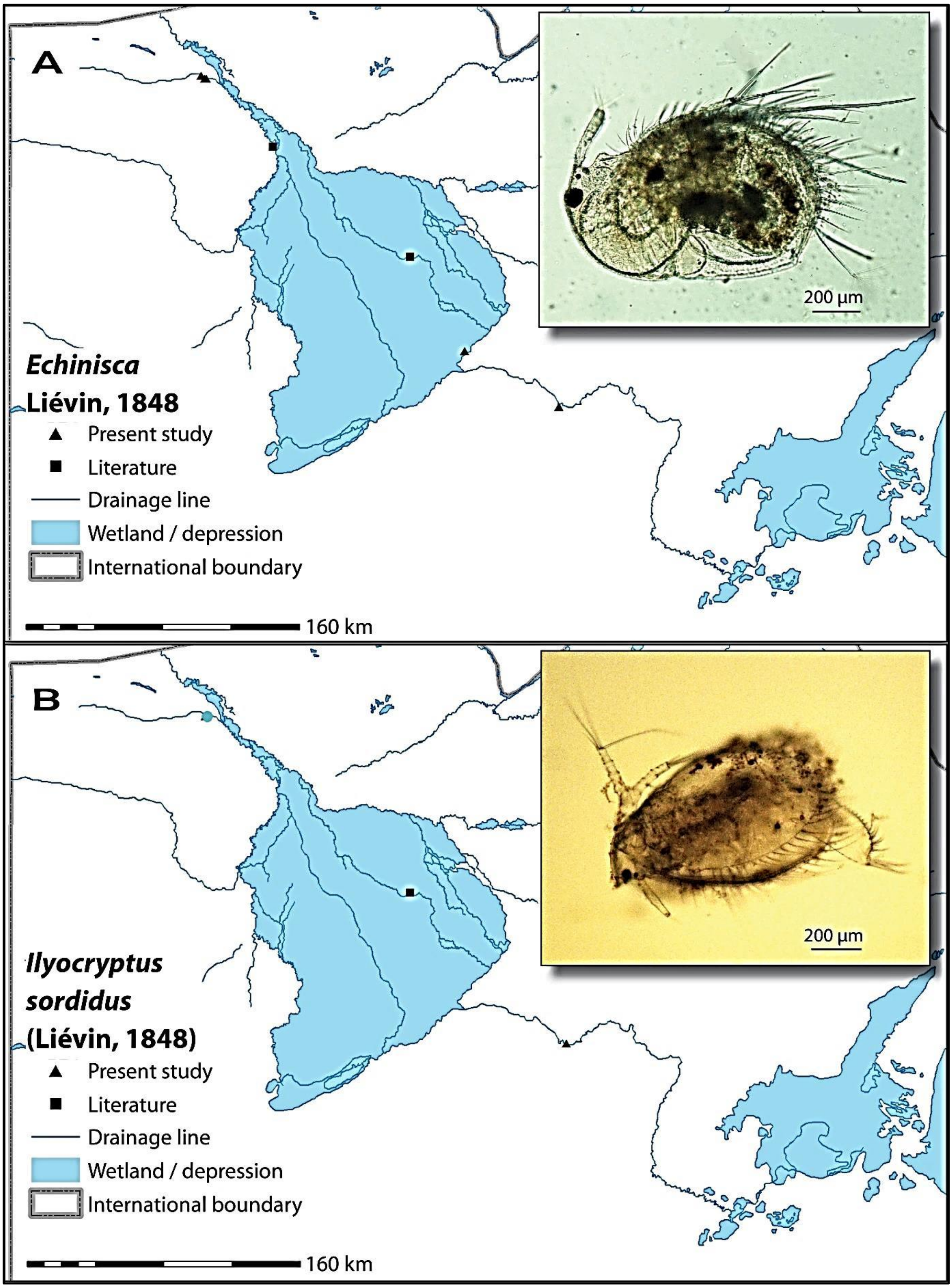

Figure 6.7: Geographic Information System (GIS) maps indicating the distribution of the cladocerans **A**: *Echinisca* Liévin, 1848 and **B**: *Ilyocryptus sordidus* (Liévin, 1848) throughout the Okavango Delta and its associated basins, Botswana.

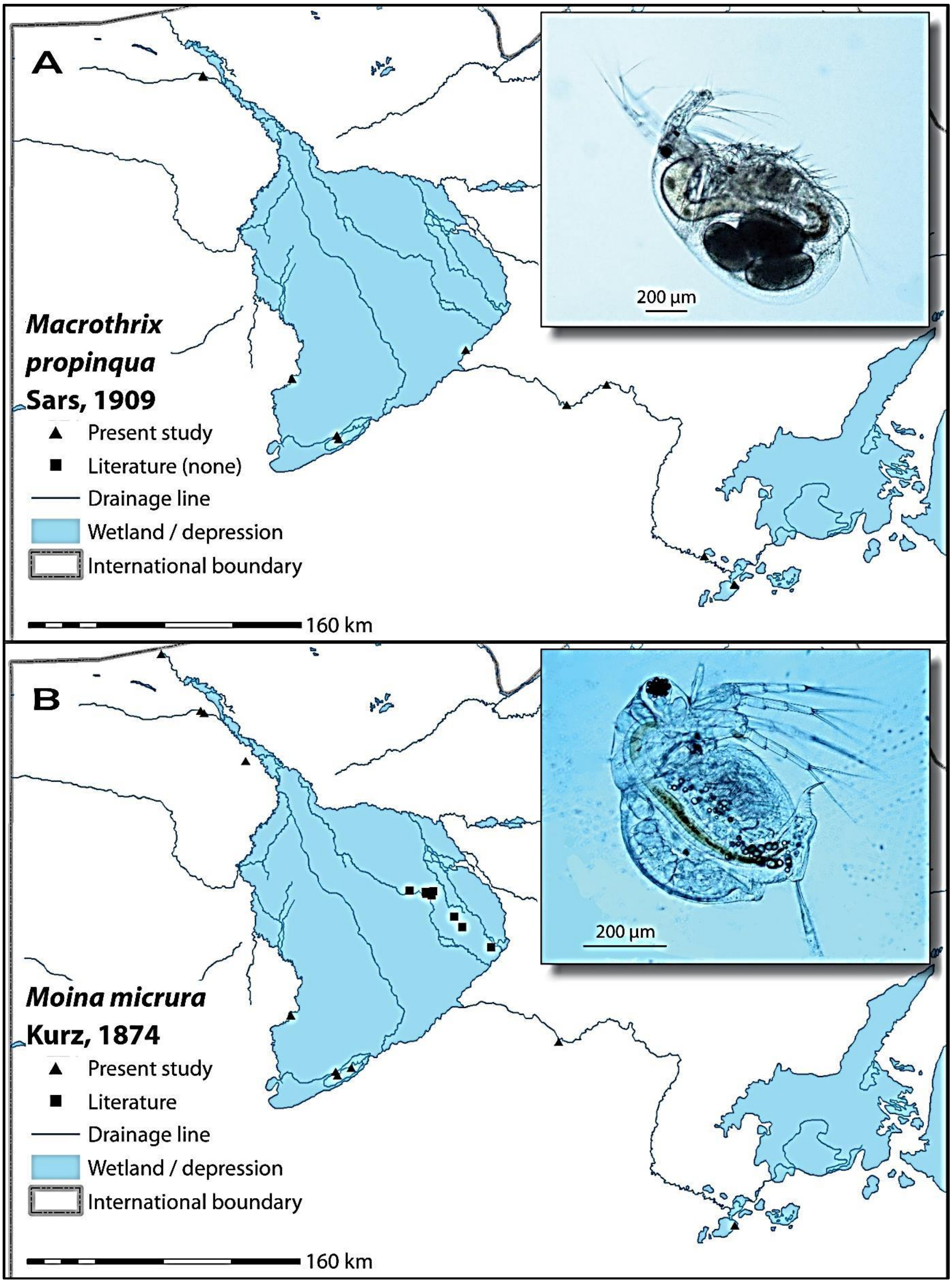

Figure 6.8: Geographic Information System (GIS) maps indicating the distribution of the cladocerans **A**: *Macrothrix propinqua* Sars, 1909 and **B**: *Moina micrura* Kurz, 1874 throughout the Okavango Delta and its associated basins, Botswana.

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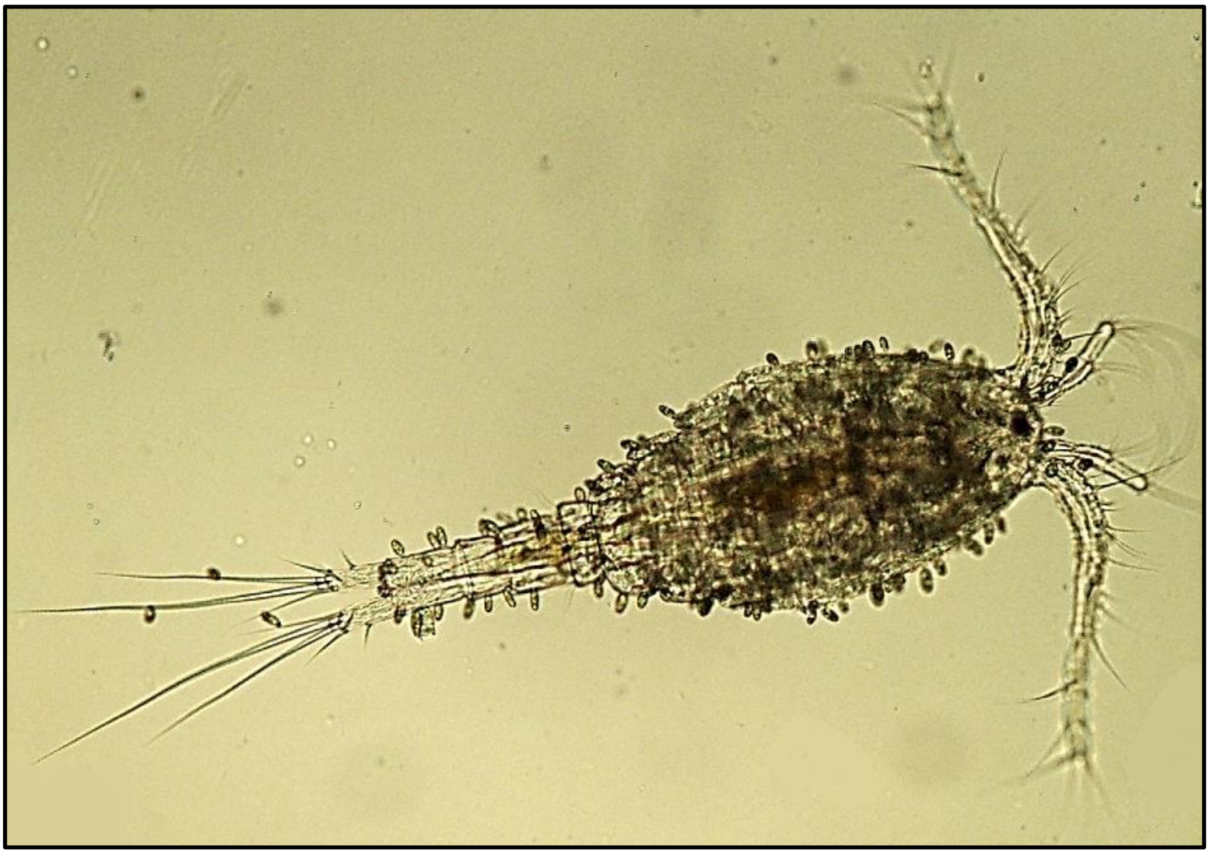
Chapter 7



TAXONOMIC ACCOUNT AND DISTRIBUTION OF COPEPODA

INTRODUCTION

Freshwater Copepoda, along with many other invertebrate groups, has been a neglected field of study in southern Africa due to a number of reasons. Studies have mainly been initiated by institutions abroad and researchers have relied heavily on material to be sent to them. Furthermore, South Africa’s political isolation, lack of researchers in the past and shortage of funding also hindered research on the subcontinent (Rayner & Heeg 1994).

More recently, taxonomic work has been conducted on members of the order Calanoida in southern Africa. Rayner (1992) revised the genus *Lovenula* Schmeil, 1898; Rayner and Heeg (1994) plotted the distribution patterns of the southern African Diaptomidae Baird, 1850; Rayner (1994; 1999a) described six new species (three species of *Tropodiaptomus* Kiefer, 1932 and three of *Paradiaptomus* Sars, 1895); Hart and Rayner (1994) described the distribution patterns of the genera *Metadiaptomus* Methuen, 1910 and *Tropodiaptomus* in relation to temperature and Rayner (2000) summarised the species belonging to the subfamily Paradiaptominae as well as their biogeography on the African Continent.

Except for a number of species described or mentioned by early researchers, such as G. Stewardson Brady, Georg Osian Sars and Frederich Kiefer between 1904 and 1934, there has been no recent taxonomic research on representatives of the orders Cyclopoida and Harpacticoida in southern Africa (Reid *et al*. 2000; Rayner 2001). Hence, attention should be given to the taxonomy of these two orders before any comments are made concerning their species composition and distribution.

In the Okavango Delta, the Copepoda are the group of zooplankton which have been neglected most. Only six studies (Hart 1997; Hart *et al*. 2003; Lindholm & Hessen 2007; Siziba *et al*. 2011a; 2011b; 2013) attempted to include the copepods of the area, most likely due to our lack of knowledge on these organisms in southern Africa. Amongst these, only Hart (1997) and Hart *et al*. (2003) included areas which are not around Chief’s Island in the Okavango Delta Fan.

Prior to the present study, the copepods, together with the cladocerans, had not been studied in the Thamalakane River and the upper Boteti River, and surveys in the Thaoge Channel, Lake Ngami, the lower Boteti River and Lake Xau have not been possible in the past 20 to 30 years due to persistent drought. Hence, this study provides the first insight to the members of the subclass Copepoda of these ephemeral water bodies. Copepod sampling sites of previous studies and that of the present study are indicated in Figure 7.1.

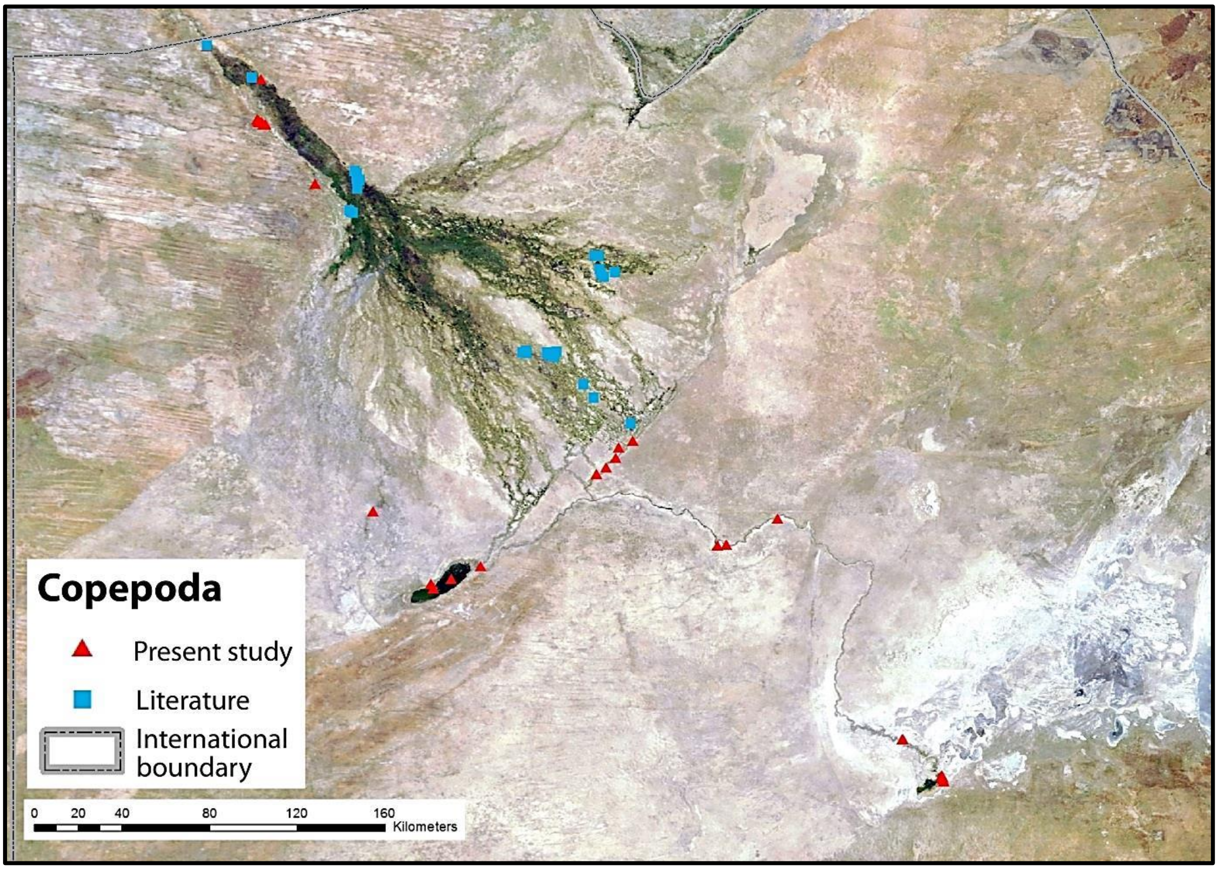


Figure 7.1: Geographic Information System (GIS) map indicating the sites within the Okavango Delta and its associated basins in northern Botswana where Copepoda samples were collected during the present study in 2011, 2012 and 2013 as well as where data was available for Copepoda from previous studies.

RESULTS AND REMARKS

Forty five Copepoda samples, collected from 38 study sites throughout the Okavango Delta and its associated basins, revealed only two genera and two species of the order Calanoida, family Diaptomidae Baird, 1850, and seven genera and eight species of the order Cyclopoida, family Cyclopidae Rafinesque, 1815 (Table 7.1). The genera of the order Calanoida included one species of *Metadiaptomus* and one of *Tropodiaptomus* (Table 7.1). The taxa of the orders Calanoida and Cyclopoida are provided in Table 7.1. and the study sites at which they were found are listed in Table 7.2.

Table 7.1: Calanoida and Cyclopoida taxa recorded in northern Botswana in 2011, 2012 and 2013.

PHYLUM ARTHROPODA	
CLASS: MAXILLOPODA	
Order Calanoida	**Order Cyclopoida**
Family Diaptomidae Baird, 1850	**Family Cyclopidae Rafinesque, 1815**
Metadiaptomus Methuen, 1910 sp.	*Ectocyclops phaleratus* (Koch, 1838)
Tropodiaptomus schmeili (Kiefer, 1926)	*Eucyclops sublaevis* (Sars, 1927)
	Mesocyclops major Sars, 1927
	Microcyclops crassipes (Sars, 1927)
	Paracyclops poppei (Rehberg, 1880)
	Thermocyclops macracanthus (Kiefer, 1929)
	Thermocyclops neglectus (Sars, 1909)
	Tropocyclops prasinus (Fischer, 1860)

Table 7.2: Distribution of Calanoida and Cyclopoida taxa collected in northern Botswana in 2011, 2012 and 2013. Taxa are presented from highest to lowest frequency. Study sites within the various water bodies are presented in a colour code as follows: 1. Okavango Panhandle, 2. Okavango Delta, 3. Thamalakane River, 4. Lake Ngami, 5. Boteti River and 6. Lake Xau. 'N' indicates the number of water bodies in which the species were present.

CLADOCERA TAXA	**STUDY SITES**	**N**
Cyclopidae Rafinesque, 1815 spp.	Mohembo Pool, Ngarangi Floodplain, NX01, NX02, NX03, NX04, NX05, NX06, NX07, NX11, NX12, Ikoga, Taoge Tsau, Maun03, Maun02, Maun04, MaunTJL, Nhabe, LN01, LN02, LN03, Makalamabedi01, Makalamabedi02, Motopi, LX01, LX02, LX03, LX04, LX05. =29	6
Tropodiaptomus schmeili (Kiefer, 1926)	Mohembo Pool, NX01, NX02, NX03, NX04, NX05, NX07, NX09, NX15, Ikoga, Thaoge Tsau, Maun03, Maun04, LN01, Makalamabedi01. =15	5
Metadiaptomus Methuen, 1910 sp.	Mohembo Pool, NX07, Ikoga, LN01, LN02, LN03. =6	2

ORDER CALANOIDA

All freshwater calanoid species of the African continent belong to the family Diaptomidae. Seven freshwater Diaptomidae genera have been recorded from the Afrotropical geographic area (Boxshall & Defaye 2008). The family Diaptomidae is split into two subfamilies, the Paradiaptominae and the Diaptominae. Six genera of Diaptomidae occur in southern Africa, four of which (*Lovenula* Schmeil, 1898, *Neolovenula* Gauthier, 1938, *Paradiaptomus* and *Metadiaptomus*) belong to the Paradiaptominae and two of which (*Tropodiaptomus* and *Thermodiaptomus* Kiefer, 1932) belong to the Diaptominae (Rayner 1999b). It is noteworthy that most species of freshwater Calanoida are extremely specific to their habitats and many species are only found in narrow geographical ranges (Rayner 2001). One African genus for example, *Camerundiaptomus* Dumont & Chiambeng, 2002, is only known from the rainforests of Cameroon and its abundance is very low (Dumont & Chiambeng 2002). Species such as *Metadiaptomus capensis* (Sars, 1907) and *Lovenula excellens* Kiefer, 1929 have only been collected from saline waters in localised areas of the Cape and Mpumalanga, South Africa, respectively (Rayner 2001).

FAMILY DIAPTOMIDAE Baird, 1850: SUBFAMILY PARADIAPTOMINAE Kiefer, 1932

All, but four, species of the subfamily Paradiaptominae are endemic to Africa (Rayner 1999b) and generally occur in the temporary waters of arid areas. Three species, *Lovenula falcifera* (Lovén, 1845), *Metadiaptomus meridianus* (van Douwe, 1912) and *Metadiaptomus colonialis* (van Douwe, 1914), however, have adapted to colonising man-made lakes (Rayner 2001).

Genus *Metadiaptomus* Methuen, 1910 (Fig. 7.2)

All species of the genus *Metadiaptomus* are endemic to Africa and Madagascar, except for two which also occur in Iran and Iraq. *Metadiaptomus* species are capable of tolerating saline waters and some are able to colonise man-made reservoirs. Although certain species have a limited distribution range, others are widely distributed in Africa (Rayner 1999b). A new species of *Metadiaptomus*, which seems to be closely related to *Metadiaptomus transvaalensis* Methuen, 1910 ([3]Rayner 2013, Personal communication), was sampled on only four occasions in the Okavango Panhandle and Lake Ngami. This undescribed species was found at Ikoga in the panhandle in 2011 for the first time. Thereafter it was present in the Mohembo Pool (Okavango Panhandle) and Lake Ngami (LN01, LN02 and LN03) in 2012 and in the Nxamasere Floodplain (NX07) (Okavango Panhandle) in 2013. In other words, it occurred in localised areas in the panhandle in 2011, 2012 and 2013 and in Lake Ngami in 2012 (Fig. 7.2). No metadiaptomid species have been recorded from the delta by previous authors (Fig. 7.2), but during the present study *M. transvaalensis* was found in the Nata River, which is discussed in **Chapter 8**.

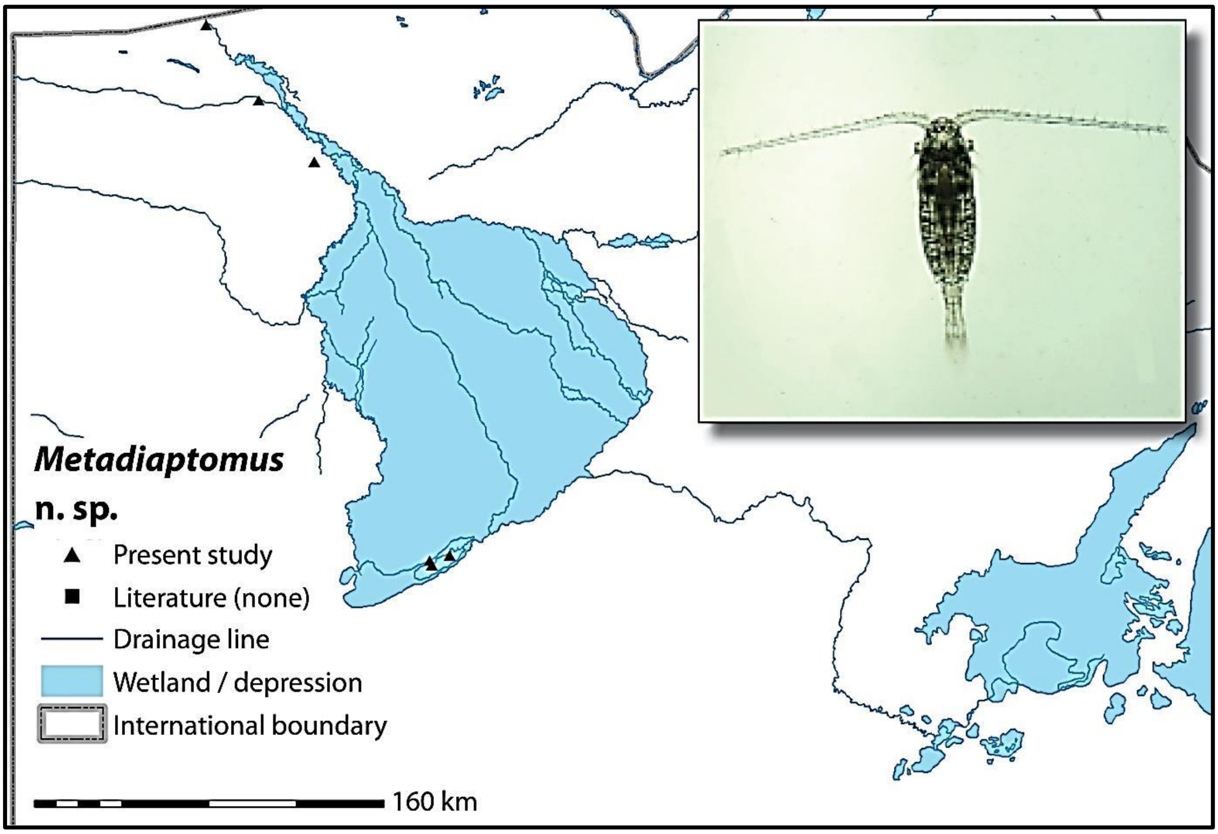


Figure 7.2: Geographic Information System (GIS) maps indicating the distribution of the calanoid *Metadiaptomus* n. sp. throughout the Okavango Delta and its associated basins, Botswana.

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FAMILY DIAPTOMIDAE Baird, 1850: SUBFAMILY DIAPTOMINAE Kiefer, 1932

Species of the subfamily Diaptominae mostly occur in the more permanent waters of the warm subtropical areas of Namibia, Botswana and eastern South Africa (Rayner 2001). The genus *Thermodiaptomus* is endemic to Africa (Rayner 2001), while *Tropodiaptomus* is widely distributed in Asia, Australia and Africa (Dussart *et al*. 1984).

Genus *Tropodiaptomus* Kiefer, 1932 (Figs. 7.3A & 7.3B)

More than 30 species of the genus *Tropodiaptomus* occur in Africa, eight of which are found in East and southern Africa. Unfortunately, many of these species have incorrectly been assigned to *Tropodiaptomus kraepilini* (Poppe & Mrázek, 1895), originally recorded from Zanzibar (Rayner 2001). *Tropodiaptomus schmeili* (Kiefer, 1926) was widely distributed throughout the study area, but was not present in Lake Xau. This species was collected on a number of occasions in the Okavango Panhandle in 2011 (NX01, NX05, NX09, NX15 and Ikoga), 2012 (Mohembo Pool, NX02, NX03 and NX04) and 2013 (NX01 and NX07). In the outer reaches of the Okavango Delta, it was present at Maun03 in 2011 and Thaoge Tsau in 2012, while it was found in the Thamalakane River (Maun04) once in 2012, in Lake Ngami (LN01) in 2011 and 2013 and in the Boteti River (Makalamabedi01) in 2011. No calanoids were sampled in the Boteti River south of the village of Makalamabedi and neither in Lake Xau (Figs. 7.2, 7.3A & 7.3B). *Tropodiaptomus schmeili* was only identified on one occasion by previous authors (Hart *et al.* 2003) from the eastern Delta Fan (Fig. 7.3A). It is widely distributed in Zimbabwe and has been collected in Namibia (Rayner & Heeg 1994; Rayner 2001) and Botswana (Hart *et al.* 2003).

Calanoid species found by previous authors in the southern end of the panhandle (Hart 1997) and the Okavango Delta Fan (Hart *et al.* 2003; Siziba *et al*. 2011a) were mostly identified as *Tropodiaptomus* species other than *T. schmeili* (Fig. 7.3B). Only three studies (Hart 1997; Hart *et al.* 2003; Siziba *et al*. 2011a) identified calanoid species from the system and Siziba *et al*. (2011a) only identified it up to genus level. Other calanoid species collected by Hart (1997) and Hart *et al.* (2003) included *Tropodiaptomus capriviensis* Rayner, 1994, *T. kissi* Dussart, 1978, *T. kraepelini* and *T. longispinosus* Einsle, 1971.

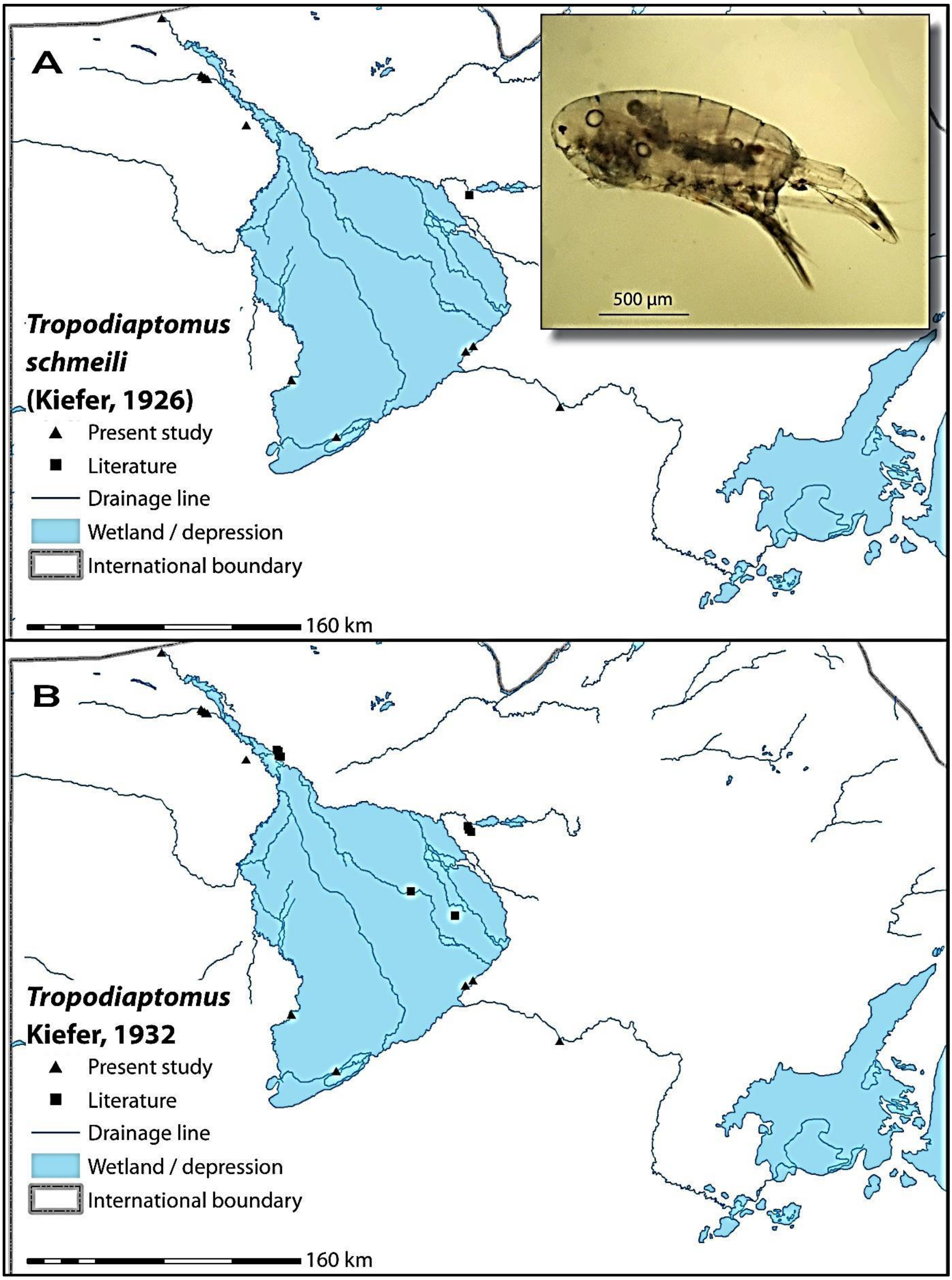

Figure 7.3: Geographic Information System (GIS) maps indicating the distribution of the calanoids **A**: *Tropodiaptomus schmeili* (Kiefer, 1926) and **B**: *Tropodiaptomus* Kiefer, 1932 spp. throughout the Okavango Delta and its associated basins, Botswana.

ORDER CYCLOPOIDA

In the Afrotropical region, all the freshwater, free-living Cyclopoida belong to the family Cyclopidae (Boxshall & Defaye 2008). Some of the species which occur in southern Africa have a world-wide distribution (Rayner 2001).

FAMILY CYCLOPIDAE Rafinesque, 1815

Karaytuğ *et al*. (2004) pointed out that there is no modern systematic study of the entire family Cyclopidae and that most genera are in pressing need of revision. They continue that this family has confusing systematics and that the systematics concept thereof continues to be based primarily on the form and armature of the fifth leg. Furthermore, they stated that only counting the number of segments in the antennules should not be used as it has been revealed that species of different genera, e.g. *Ectocyclops phaleratus* (Koch, 1838) and *Paracyclops canadensis* (Willey, 1934), have the same number of segments, but do in fact have other morphological differences (Karaytuğ *et al*. 2004).

In his attempt to better define the genera of the subfamily Cyclopinae by combining the structure and setation of the fifth leg with other morphological features, Pesce (1996) mentioned that there is no world review of this subfamily and neither is there an updated identification key for the known genera. In his opinion, the present confusion among members of the subfamily is largely because vital micro-characters, which were not considered important in the past, are still neglected in descriptions and illustrations. Furthermore, numerous species and genera have been inadequately described and it has been discovered that a number of taxa combine morphological characteristics of different genera, which further complicates our understanding of this group of organisms (Pesce 1996). The diagnosis of many genera of the subfamily Cyclopinae remains unclear and contentious and the origin of many taxonomic problems within the family as a whole are due to researchers randomly including new species into particular genera (Karaytuğ *et al*. 2004).

Cyclopoida species from the Okavango Delta and its associated basins have been identified by previous authors as *Ectocyclops* spp. (Siziba *et al*. 2011a), *Eucyclops euacanthus* (Sars, 1909) (Hart *et al.* 2003), *Eucyclops (Afrocyclops) gibsoni* (Brady,

1904) (Hart *et al.* 2003), *Eucyclops serrulatus* (Fischer, 1851) (Hart *et al.* 2003), *Macrocyclops albidus* (Jurine, 1820) (Siziba *et al*. 2011a), *Macrocyclops viridus* (this may be an error, as no such species can be found) (Siziba et al 2013), *Mesocyclops leuckarti* (Claus, 1857) (Lindholm & Hessen 2007; Siziba *et al.* 2011a; 2011b; 2013), *Mesocyclops major* Sars, 1927 (Hart 1997; Hart *et al.* 2003), *Microcyclops crassipes* (Sars, 1927) (Hart *et al.* 2003), *Microcyclops rubelloides* Kiefer, 1952 (Hart *et al.* 2003), *Microcyclops varicans* (Sars, 1863) (Hart *et al.* 2003; Siziba *et al.* 2011a; 2011b; 2013), *Paracyclops ?fimbriatus* (Fischer, 1853) (Hart *et al.* 2003), *Thermocyclops neglectus* (Sars, 1909) (Hart *et al.* 2003) and *Thermocyclops oblongatus* (Sars, 1927) (Hart 1997).

In the present study, members of the family Cyclopidae were found in all the water bodies within the study area (Table 7.2). Table 7.1 provides a list of the members of the family Cyclopidae that were collected from the Okavango Delta and its associated basins. These species include *Ectocyclops phaleratus* (Koch, 1838), *Eucyclops sublaevis* (Sars, 1927), *Mesocyclops major* Sars, 1927, *Microcyclops crassipes* (Sars, 1927), *Paracyclops poppei* (Rehberg, 1880), *Thermocyclops macracanthus* (Kiefer, 1929), *Thermocyclops neglectus* (Sars, 1909) and *Tropocyclops prasinus* (Fischer, 1860). Five of the eight species of cyclopoids, namely *Ectocyclops phaleratus, E. sublaevis, P. poppei, T. macracanthus* and *T. prasinus,* were recorded from the Okavango Delta and its associated basins for the first time. It must be added, however, that more identification characters are needed to establish a rigorous diagnosis of the genera of Cyclopidae and this can only be achieved with detailed species descriptions (Karaytuğ *et al*. 2004).

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Chapter 8

THE NATA RIVER

The Nata River in north-eastern Botswana is a seasonal river with an average annual flow of more or less 279 million m³. It is an important resource in its semi-arid setting, yet information on the biological diversity of the Nata River is scarce and no such information is available on its invertebrate fauna. The Nata River is connected to the Okavango System in that the Makgadikgadi Pans act as the final sink for the water of both rivers. The Nata is, however, a completely different system which flows off the Zimbabwean Plateau and has a water chemistry very different to that of the Okavango River System. It has, therefore, been dealt with as a separate entity in the present study. This chapter provides the first record of the aquatic micro-invertebrates and physical water quality in the lower reaches of the Nata River during the dry season. Furthermore, during sampling of zooplankton from the Nata River, the mobiline epibiont, *Trichodina diaptomi* Šrámek-Hušek, 1953, associated with copepods of the order Calanoida, was observed on the carapace of *Metadiaptomus* *transvaalensis* Methuen, 1910. Members of the genus *Trichodina* Ehrenberg, 1830 are mainly associated with freshwater fish, but on only a few occasions have been found associated with different species of freshwater planktonic copepods, amongst other aquatic organisms. The occurrence of *T. diaptomi* in a system that most definitely dries up annually and on organisms which have diapausing stages that enable them to withstand periods of desiccation has brought to mind many questions concerning the life-history of trichodinids.

This chapter is presented in the form of two scientific papers prepared for the journals *African Journal of Aquatic Science* and *Acta Parasitologica*, respectively, and the formatting of each of these is according to the instructions to authors for each of the journals. However, the headings of the papers have been adapted to fit the format of the rest of this document. The first paper deals with the zooplankton composition of the lower Nata River during the dry season and has been prepared for submission to the *African Journal of Aquatic Science*. The second paper provides the first record of *T. diaptomi* from calanoid copepods in Botswana and includes another population of this epibiont from a dam in South Africa. This paper includes remarks on the life-history of *T. diaptomi* and has been accepted for publication in *Acta Parasitologica*.

ZOOPLANKTON COMPOSITION OF THE LOWER NATA RIVER, BOTSWANA, DURING DRY SEASON

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ABSTRACT

The Nata River is a seasonal river, situated in the semi-arid region of north-eastern Botswana where the rainfall is unpredictable and drought is a fairly common occurrence. Nevertheless, its annual flow of about 279 million cubic meters is significant by eastern Botswana standards and it forms an important source of life for the local people of the region. Information on the biological diversity of the Nata River is scarce and to our knowledge no such data is available on the invertebrate fauna of the river. The aim of the study was to provide the first record of the aquatic micro-invertebrates and physical water quality characteristics of the lower Nata River during dry season, which may contribute to future monitoring thereof. In August 2012 physical water quality parameters were measured and zooplankton sampled. The four sites sampled ranged widely in salinity, TDS and electrical conductivity in particular. Additionally, a total of 14 species of Copepoda, Cladocera and Rotifera were collected and it was found that the species composition differed remarkably between the study sites, mainly due to the restriction brought about by salinity. The species abundance during the survey was probably at its annual lowermost and not at all a complete census of the species.

Keywords: Calanoida, Cladocera, diversity, physical parameters, Rotifera, water quality

INTRODUCTION

The Nata River (as it is known in Botswana), or the Amanzanyama River of Zimbabwe, helps to replenish aquifers and is an important source of life for the local people of the region. It flows off the Zimbabwe Plateau in a south-westerly direction and eventually enters Sua Pan, one of the massive pans of the Makgadikgadi Pans complex. As is true for the entire Botswana, the climate in the region of the Nata is semi-arid. The rainfall is low, ranging between 240 mm and 700 mm and averaging 400 to 450 mm annually, and comes in the form of short, intense thundershowers. On the other hand, evaporation rates are high and at times may be as much as eight to ten times that of the rainfall input to the Kalahari. The wet season is from November to April, but rainfall in the area is very unpredictable and drought is a fairly common occurrence (Hitchcock & Nangati 2000; Hitchcock 2003).

The Nata River has a catchment of 23,000 km^2, most of which is in Zimbabwe, and an annual flow of 279 million m^3. This represents a significant resource by eastern Botswana standards (Hitchcock 1995, 2003; Hitchcock & Nangati 2000). The rivers in north-eastern Botswana and western Zimbabwe are ephemeral and the Nata River is the largest of these, with two smaller rivers as tributaries, namely the Dzivanini and Sa/a Rivers. Not only is the Nata seasonal, it also experiences long-term variations in flow. During some years when rainfall is high, the river may flow for extended periods, while on the other hand it may not flow at all, sometimes for several years, during periods of drought. These long-term climatic changes and droughts have significant impacts on the faunal, floral, livestock and human populations in the region (Hitchcock 2003).

Peak flow in the Nata is generally between January and March annually, at which time it flows into its delta in Sua Pan. Large numbers of flamingo and other waterfowl congregate in a shallow lake, 400-600 km^2 in size, within the Nata Delta, to feed and breed (Hitchcock 1995; Hitchcock & Nangati 2000). Hence, the Nata Sanctuary was established in the late 1980's. It is a conservation area which covers 230 km^2, located in the northern tip of Sua Pan, and incorporates the southern part of the Nata River and what is known as its delta. The lower reaches of the Nata contain brine pools in which salt of an extremely high quality is formed (Hitchcock 2003).

Information on the biological diversity of the Nata River is scarce and to our knowledge no such data is available on the invertebrate fauna thereof. Data is available on the hydrochemical fluctuations and crustacean community composition in Sua Pan of Lake Makgadikgadi (Seaman et al. 1991; McCulloch et al. 2008). There is no record of the Rotifera composition of either the Makgadikgadi Pans or of the Nata River. The present study aims at providing baseline data and the first record of the aquatic micro-invertebrates and physical water quality characteristics of the lower Nata River during the dry season and low water levels, which will contribute to future monitoring thereof. This study not only includes micro-crustaceans, but Rotifera as well. It also provides a checklist of species recorded from the Nata River and its end-point, the Makgadikgadi Pans.

MATERIALS AND METHODS

STUDY SITES

The survey was conducted in August 2012 from a basecamp in the village Nata in North-eastern Botswana (Figures 1A & 1B). At this time the ephemeral river was at low water levels and had begun to dry, leaving behind pools of various sizes and salinity. Sampling took place in a number of these pools along the course of the Nata River in and around Nata Village (Figures 1A & 1B). Nata01 (20°12’17” S, 26°11’18” E) and Nata04 (20°11’07” S, 26°11.12” E) were situated within a part of the river which still held a comparatively significant volume of water, but already formed a pool, as it was cut-off from water upstream and downstream of it. Here, livestock came to drink and waded in the water. Nata02 (20°12’37” S, 26°11’16” E) was a small saline pool south of Nata01 and Nata04, while Nata03 (20°12’55” S, 26°11’07” E) was the most southerly of the sampling stations and closest to the Nata Delta, with the highest salinity.

SAMPLE COLLECTION

A Hanna HI 9828 Multiparameter, which was calibrated on a regular basis according to the manufacturer’s specifications, was used to measure physical water quality parameters at all study sites. These parameters included water temperature, pH, dissolved oxygen concentration, conductivity, total dissolved solids and salinity.

Zooplankton was sampled from open waters and between aquatic vegetation by swooping a hand-held net, with a 50 µm pore aperture and a mouth diameter of 35 cm, vertically and horizontally through the water to cover different depths. Most pools, however, had a limited depth and zooplankton analysis was qualitative only. After collection, samples were transported to a temporary field laboratory in Nata Village where live observations were made using a Nikon Eclipse E100 and a Nikon SMZ800 light microscope and micrographs were taken using a Nikon DS-Fi1 camera which can be attached to both the compound and dissecting microscopes. Samples were halved and fixed in 70% ethanol and 4% formaldehyde solutions for long-term preservation and later identification. Zooplankton were identified using Sars (1916; 1927), Ruttner-Kolisko (1974), Nogrady et al. (1993), Kořínek (1999), Seaman et al. (1999) Rayner (1999; 2001), Ricci and Melone (2000) and Brain (2002). Species identified include representatives from the Calanoida, Cyclopoida, Cladocera and Rotifera, but exclude the Ostracoda, which have been collected for future analyses. All material, including Ostracoda, has been deposited in the collection of the Aquatic Ecology Research Group of the Department of Zoology and Entomology, University of the Free State, South Africa.

RESULTS

NATA01 (Figure 1B)

Nata01 had an arithmetic mean temperature of 17.51 °C. The water of the lower Nata was alkaline with an average pH of 8.54 at Nata01. Dissolved oxygen concentrations were high, averaging 119.7%. The mean conductivity, total dissolved solids and salinity were 1.33 mS/cm, 667 ppm and 0.67 PSU, respectively. Water quality results are summarised in Table 1. A total of 13 zooplankton species were sampled from Nata01 which included a calanoid, *Metadiaptomus transvaalensis* Methuen, 1910, a cyclopoid, *Eucyclops sublaevis* (Sars, 1927), a cladoceran, *Moina micrura* Kurz, 1874, and 10 rotifer species, namely: *Asplanchna brightwelli* Gosse, 1850; *Brachionus caudatus austrogenitus* Ahlstrom, 1940; *B. calyciflorus* Pallas, 1766; *B. falcatus* Zacharias, 1898; *Conochilus coenobasis* (Skorikov, 1914); *Filinia longiseta* (Ehrenberg, 1834); *F. opoliensis* (Zacharias, 1898); *Keratella tropica* (Apstein, 1907); *Lecane papuana* (Murray, 1913) and *Rotaria neptunia* Ehrenberg, 1832 (Figures 2 & 3, Table 2).

NATA02 (Figure 1B)

The arithmetic mean water temperature at Nata02 was 17.17 °C, while the pH was alkaline with a reading of 9.46. The high oxygen levels at this site averaged 148.8%. The mean conductivity, total dissolved solids and salinity were much higher than at Nata01 with readings of 24.46 mS/cm, 12,550 ppm and 15.25 PSU, respectively (Table 1). Only one species of zooplankton, the cladoceran *Moina belli* Gurney, 1904 (Fig 2E) (Table 2), was identified from Nata02. Ostracoda were also present in this saline pool.

NATA03 (Figure 1B)

The arithmetic mean readings for temperature, pH, dissolved oxygen concentration, conductivity, total dissolved solids and salinity at Nata03 were 19.72 °C, 9.26, 73.5%, 149.8 mS/cm, 74,900 ppm and 70 PSU, respectively (Table 1). No zooplankton species were present in Nata03 (Table 2).

NATA04 (Figure 1B)

The physical water quality mean values at Nata04 were 18.33 °C, 8.68, 120.2%, 2.22 mS/cm, 1,112 ppm and 1.15 PSU for temperature, pH, dissolved oxygen concentration, conductivity, total dissolved solids and salinity, respectively (Table 1). A total of 10 zooplankton species were identified from Nata04 which included a calanoid (*Metadiaptomus transvaalensis*), a cyclopoid (*Eucyclops sublaevis*), a cladoceran (*Moina micrura*) and seven rotifer (*Brachionus caudatus austrogenitus*, *B. calyciflorus*, *Filinia longiseta*, *F. opoliensis, Keratella tropica, Lecane papuana* and *Rotaria neptunia*) species (Figures 2 & 3, Table 2).

DISCUSSION

At the time of sampling (August 2012), species richness in the lower Nata River was extremely low with a total of 14 species (excluding Ostracoda) (Figures 2 & 3, Table 2) collected. The species abundance at this time, however, was probably at its annual lowermost and not at all a complete census of species in the lower Nata River. Temporary rivers, such as the Nata River, undergo tremendous changes through a hydrological cycle as they go through a running water period and then start forming shallow ponds and deeper pools before entering into a dry phase. Zooplankton species are only present when the environment is suitable and since all species have different requirements, not all are active in the water body at the same time. Ecological succession therefore takes place amongst species during the wet period.

Furthermore, hydrological fluctuations of ephemeral dryland rivers are so large that the water body hardly ever remains the same from year to year, hence zooplankton community patterns may change annually (Crispim et al. 2014). Green (2003) pointed out that in order to achieve a complete census of rotifers, for example, it is necessary to sample at different seasons, at all sub-environments, and to include both resting eggs from sediment as well as gut content of predators.

In the present study, sampling took place during the dry season at which time the river was in the process of desiccation and the waterbodies fragmented and disconnected causing environmental factors such as the physical water quality in the different pools to diversify and rapidly change. Tremendous alterations such as these, from running water to deep and shallow pools and eventually complete drought, are characteristic of temporary rivers (Crispim et al. 2014) and are the defining features of such habitats (Walsh et al. 2014). On the one hand habitats disappear and the physical and chemical water quality changes as water evaporates or percolates into the ground, while on the other hand these conditions may also be altered rapidly with the addition of large volumes of water (Walsh et al. 2014).

Zooplankton, however, poses mechanisms which enable them to tolerate adverse conditions such as desiccation or high salinity. Wetland sediments contain a reservoir of dormant stages of aquatic micro-invertebrates. Bdelloid rotifers, such as *Rotaria neptunia*, escape periods of desiccation by means of cryptobiosis, a process by which they slowly dry out and come to life again when the water body is inundated. In this state, the head and foot of bdelloid rotifers are withdrawn into the trunk, resembling a creased barrel, and they may remain viable that way for more than 20 years. On the other hand, recovery from it may take place between 10 minutes and a number of hours, depending on environmental conditions (Wallace & Snell 1991). Monogonont rotifers do not undergo cryptobiosis, but form resting eggs during unfavourable conditions (Brain 2002). Mictic females produce small haploid eggs via meiosis and if not fertilised they develop into haploid dwarf males. However, if these eggs are fertilised they become diploid and develop into resting eggs which consist of thick, sometimes sculptured, highly resistant shells around a zygote (Ruttner-Kolisko 1974; Wallace & Snell 1991; Brain 2002; Schröder 2005). Similarly, the cladocerans produce male offspring when conditions are unfavourable which results in mating and the formation of fertilised resting eggs. These eggs too are encased by a hard, resistant shell, known as the ephippium, and in a number of families, it is protected by the moulted carapace of the mother

(Seaman et al. 1999). Copepods avoid adverse periods by entering diapause either in the form of resting eggs or dormant copepodid stages (Hairston & Bohonak 1998; Rayner 2001). It is known that members of the family Cyclopidae mostly diapause as copepodids (Hairston & Bohonak 1998), while the typical dormant stage of calanoid copepods such as *Metadiaptomus transvaalensis* (Figures 2A & 2B) is diapausing eggs (Gyllström & Hansson 2004).

The dormant life stages of freshwater invertebrates described, form a reserve of latent species and genotypes *in situ*. Recruitment from the regional species pool as well as the local dormant species pool is essential for the recolonisation of aquatic environments, after disturbance events such as drying, and has important consequences for the assembly of communities as it facilitates dispersal in space and in time (Vanschoenwinkel et al. 2010). Therefore, the resting stages do not only provide a refuge during periods of drought, but conserve species and community diversity (Nielsen et al. 2003).

Vanschoenwinkel et al.'s (2010) findings supported the concept that habitats which experience more severe disturbance regimes have a lower species diversity, such as the Nata River. This may be because frequent disturbance may lead to the strict selection of a limited number of tolerant species (Vanschoenwinkel et al. 2010). Duration and timing of inundations are fundamental in the structuring of temporary aquatic habitats, as demonstrated in this case by the difference in community structure between the different study sites. Nata01 and Nata04 for example have a longer duration of inundation than Nata02 and Nata03 (Figure 1B), which can be seen in the difference in species composition and abundance (Table 2). This is largely due to the different development phases (and hence succession phases) that the respective pools were in at the time of sampling.

On the other hand, different water quality parameters, such as salinity, directly or indirectly influence the community structure in aquatic environments (Williams 1998). For example, salinity plays a major role in determining rotifer species diversity and dominance as an increased salinity reduces species diversity (Green 1993). In saline ephemeral environments, salinity shapes the recolonisation dynamics after desiccation as the change in salinity throughout a season may determine which species emerge from the dormant species pool (García-Roger et al. 2008). During the present study, the water quality was extremely diverse from one pool to the next (Table 1). The larger pools such as the one in which Nata01 and

Nata04 were situated (Figure 1B) displayed a water quality almost typical of freshwater systems in the area, while the smaller pools, no further than a few meters away, (such as Nata03 and Nata04) exhibited a water quality close to that of the Makgadikgadi Pans. The most distinct differences were in the conductivity, TDS and salinity of the various pools, with a significant increase from the largest, upstream pool to the smallest pool closest to the pans (Table 1).

With the increase in conductivity and salinity there was a decrease in zooplankton species diversity. The largest, freshwater pool had a total of 13 species compared to the one single species at Nata02 and no species in Nata03. This parallels the statement by Williams (1998) that there is an inverse correlation between species diversity and salinity, in that when salinity increases, the species diversity decreases. In a study on the zooplankton and diatoms of temporary and permanent inland pans in South Africa, Riato et al. (2014) found that the freshwater temporary pans had the highest species diversity, while the highly saline permanent pans had the lowest.

At some point in time, however, these habitats in the Nata River were connected, but it is very unlikely that species such as *Moina belli* (present in Nata02) would have been present in the connected habitat, as the water would have had a lower salinity and conductivity whilst in the flowing phase. Hence, this is most likely not an example of the most tolerant species being able to survive higher salinities and being the last remaining species in this pool. *Moina belli* prefers saline environments and the increase in salinity would have rather been a cue for this species to hatch. This is further supported by the fact that *M. belli* was not present in Nata01 and Nata04 in the freshwater pool. If it were the last remaining species, it would most likely be found in Nata01 and Nata04 too. From a survival point of view, hatching after the "favourable conditions" are over is an advantageous characteristic in the sense that less predators may be present. No fish or other predatory invertebrates were sampled from Nata02 for example. The majority of *M. belli* individuals sampled from Nata02 (Figure 2D) had produced diapausing eggs in an ephippium which is a modified part of the carapace and is shed as the mother moults (Gyllström & Hansson 2004). They most likely appear from resting stages, rapidly reproduce, produce new diapausing stages and disappear again.

Other species sampled from the Lower Nata River, such as *Metadiaptomus transvaalensis*, are tolerant of very high salinities and have been found in salt pans across southern Africa

(Seaman et al. 1991; McCulloch et al. 2008; Ferreira et al. 2012; Riato et al. 2014), including the Makgadakgai Pans (Seaman et al. 1991; McCulloch et al. 2008), as well as in slightly saline and relatively fresh water bodies such as the pool in which Nata 01 and Nata04 were situated in the present study.

It is not possible to compare the results of the present study with that of studies conducted in the Makgadikgadi Pans south of the Nata River for all groups of zooplankton as the Ostracoda were not identified during the presents study and Rotifera were not identified during studies by Seaman et al. (1991) and McCulloch et al. (2008) conducted in the Makgadikgadi (Table 3). When comparing species of Cladocera and Copepoda, however, it is clear that species in the system range from those with a wide tolerance for salinity to those that either thrive in freshwater or highly saline inland waters. As previously mentioned, *Metadiaptomus transvaalensis* has a wide tolerance range for salinity and it was present in the freshwater sites, Nata01 and Nata04 during the present study as well as in the highly saline Makgadikgadi Pans during studies conducted by Seaman et al. (1991) and McCulloch et al. (2008) in this shallow expanse of water (Table 3). Although *Moina belli* was found in both the Nata River (present study) and Makgadikgadi Pans (McCulloch et al. 2008), it was sampled in a highly saline pool only in the Nata River (Nata03), indicating that this species has a preference for waters of high salinity. *Moina micrura* and *Eucyclops sublaevis*, on the other hand, were only collected in the freshwater sites in the Nata River.

This does not necessarily mean that these species are either freshwater or saline species, as *Mesocyclops leuckarti* (Claus, 1857), which in this case was only collected in the saline Makgadikgadi Pans (Seaman et al. 1991) has been identified from the Okavango Delta (Lindholm & Hessen 2007; Siziba et al. 2011a, 2011b, 2013), the water of which is extremely fresh. The fact that it was present in the Makgadikgadi Pans and not in the Nata River may be due to the season in which samples were collected.

The phylum Rotifera was the most speciose group of organisms in the lower Nata River, although none were found in the saline Nata02 and Nata03 sampling sites (Table 2). This once again points at the effect high salinity and geographical setting have on species diversity. In their study on the rotifers of the Kgalagadi Transfrontier Park (formerly known as the Kalahari Gemsbok National Park), South Africa, Brain et al. (1995) found that despite the large differences in water quality between study sites (which included boreholes and troughs), the rotifer diversity in the area was very low and that pH did not affect the distribution of rotifers as did salinity and conductivity.

Factors, other than the duration and timing of inundation and water quality, which also affect the distribution patterns of zooplankton in saline waters include predation, food availability, competition and other biological interactions (Williams 1998). Williams (1998) pointed out that although studies on predation have indicated that biological interactions are indeed effective in determining the biological communities of saline waters, we are a long way from determining the extent to which it does.

Walsh et al. (2014) stated that much work remains to be done in order to truly understand the ability of aquatic invertebrates to withstand the rapid changes which take place in ephemeral systems. There is an international scarcity of research on the zooplankton of arid and semi-arid environments. Little is known about the zooplankton species diversity of arid zone rivers, not to mention their responses to irregular patterns of flooding and drought as well as water quality changes, particularly salinity (Shiel et al. 2006). Given their importance as vital link in the aquatic food chain, as grazers of phytoplankton and a major food source for planktivorous fish, larger invertebrate predators and filter-feeding birds it is important that we understand the effects that reduced flooding and changes in water chemistry may have on zooplankton communities and dynamics.

CONCLUSION

Increased salinity and a shorter period of inundation, amongst other factors, reduces the abundance and diversity of zooplankton taxa emerging from sediments in ephemeral dryland rivers. This may explain the low zooplankton species diversity of the lower Nata River as well as the grave difference in diversity amongst the study sites, which displayed a large difference in water quality. In temporary rivers, such as the Nata, which undergo tremendous changes through a hydrological cycle and from year to year, zooplankton community patterns do not remain constant throughout the wet phase and may differ annually. In order to achieve a complete census of zooplankton species, it is necessary to sample at different seasons, at all sub-environments and include resting eggs from the sediment. The information from this study, however, provides the first record of zooplankton in the Nata River and forms a baseline for future studies on the zooplankton species diversity and succession in response to changing water quality between the flooding and drying cycles of this ephemeral, dryland river.

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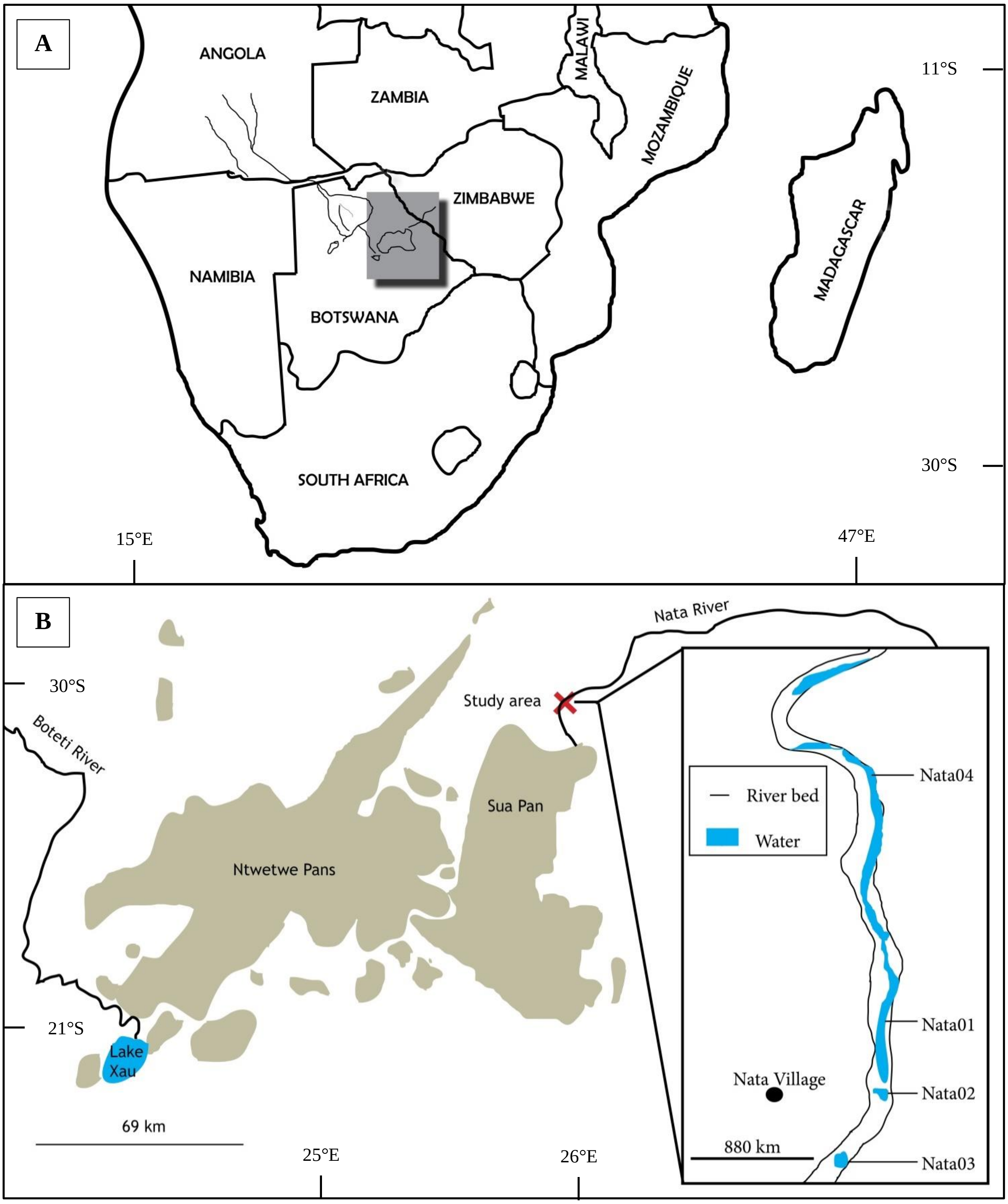

Figure 1: (A) Map of southern Africa indicating the position of Botswana and that of the Nata River and Makgadikgadi Pans within this land-locked country. (B) Map of the Nata River and Makgadikgadi Pans indicating the study area and four sampling sites in the lower Nata River.

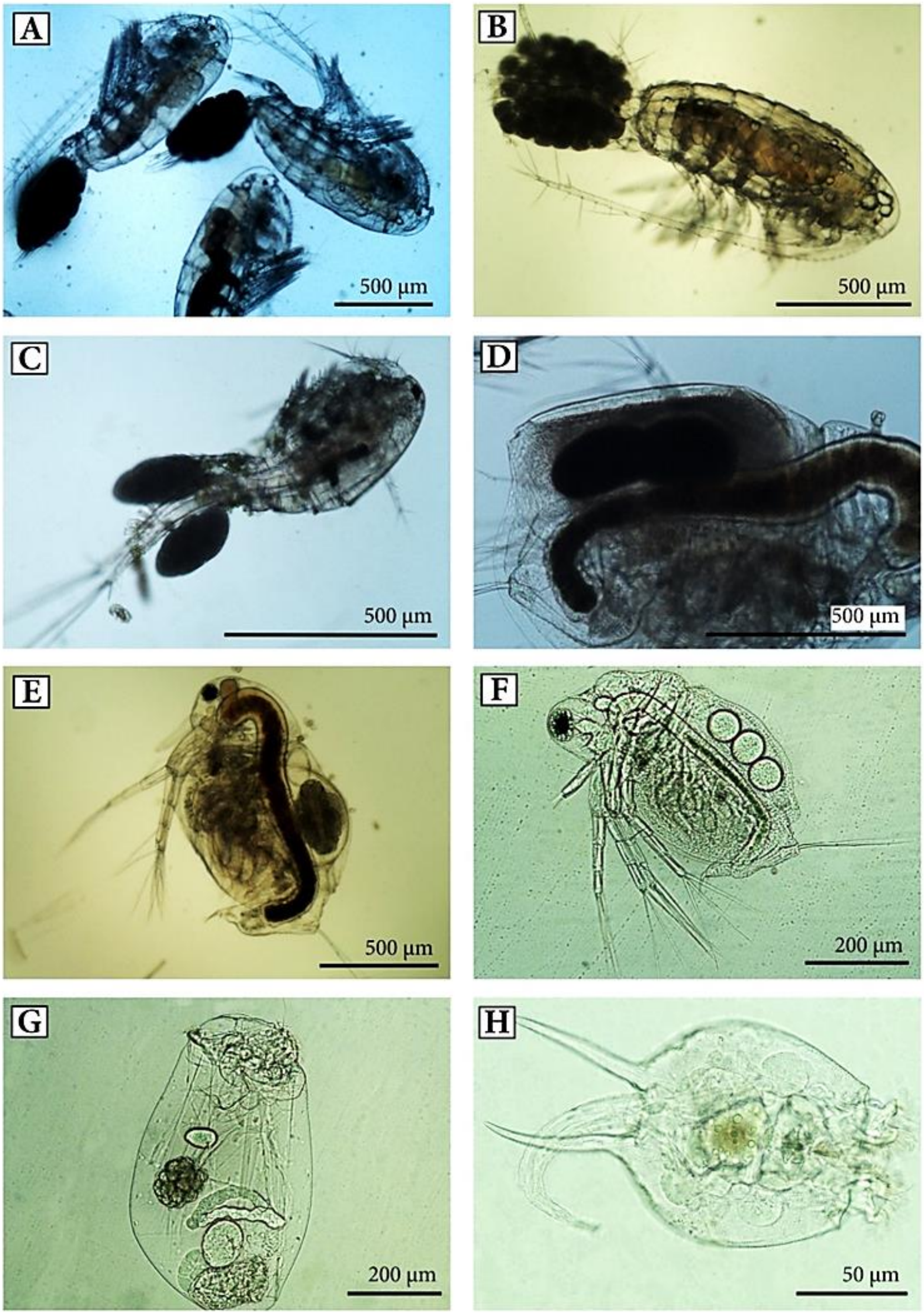

Figure 2: Light micrographs of micro-invertebrates sampled from the lower reaches of the Nata River in August 2012 at low water levels. (A&B) *Metadiaptomus transvaalensis* Methuen, 1910, breeding adult females, (C) *Eucyclops sublaevis* (Sars, 1927), breeding female, (D) Ephippia of *Moina belli* Gurney, 1904 containing two resting eggs, (E) *Moina belli*, (F) *Moina micrura* Kurz, 1874, (G) *Asplanchna brightwelli* Gosse, 1850, (H) *Brachionus caudatus austrogenitus* Ahlstrom, 1940.

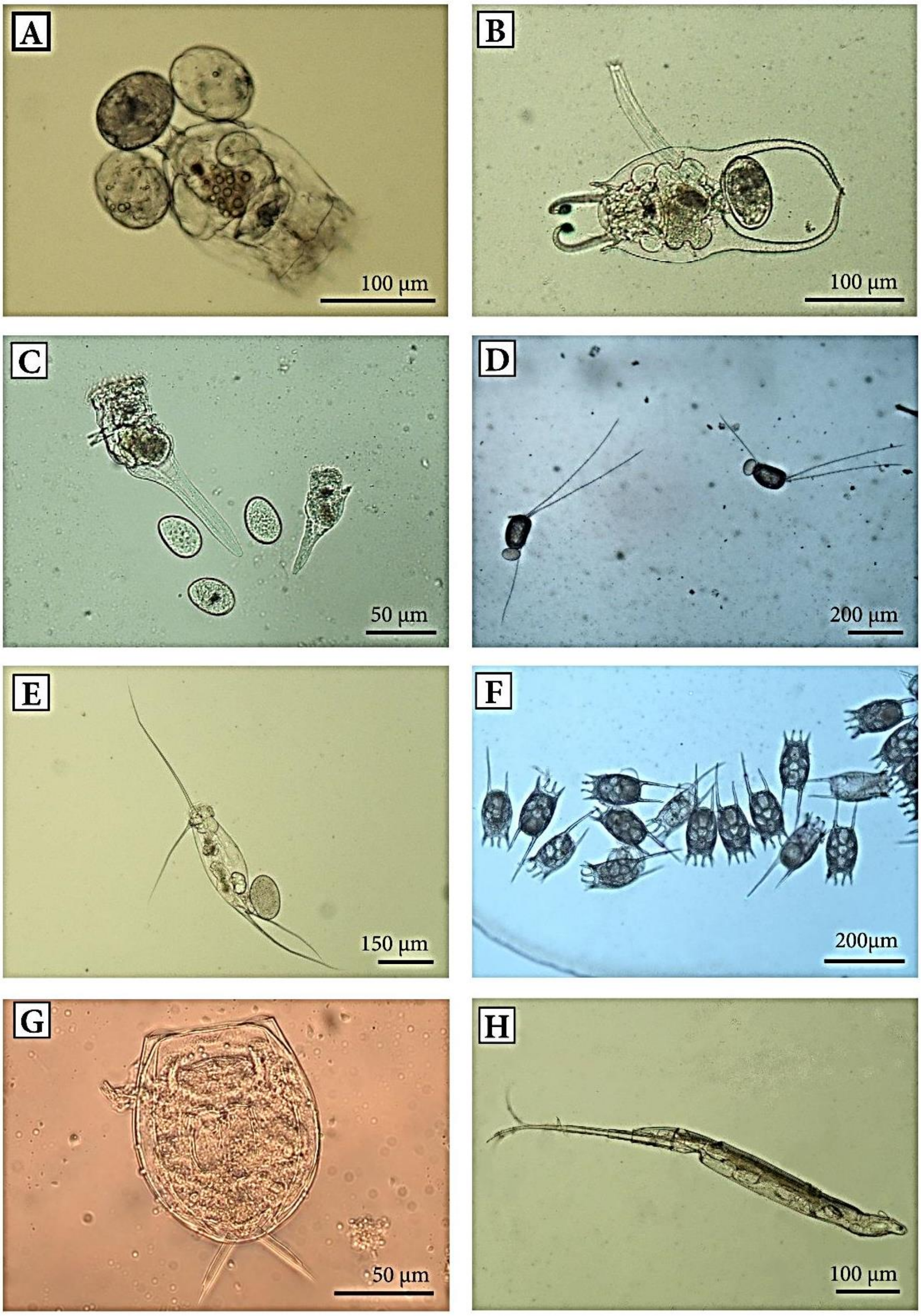

Figure 3: Light micrographs of Rotifera sampled from the lower reaches of the Nata River in August 2012 at low water level. (A) *Brachionus calyciflorus* Pallas, 1766, (B) *Brachionus falcatus* Zacharias, 1898, (C) *Conochilus coenobasis* (Skorikov, 1914), (D) *Filinia longiseta* (Ehrenberg, 1834), (E) *Filinia opoliensis* (Zacharias, 1898), (F) *Keratella tropica* (Apstein, 1907), (G) *Lecane papuana* (Murray, 1913), (H) *Rotaria neptunia* Ehrenberg, 1832.

Table 1: Physical water quality arithmetic mean values at each of the four sampling sites in the lower Nata River at low water levels (August 2012).

Physical Water Quality Parameters	Nata01	Nata02	Nata03	Nata04
Temperature (°C)	17.51	17.17	19.72	18.33
pH	8.54	9.46	9.26	8.68
Dissolved Oxygen (%)	119.7	148.8	73.5	120.2
Conductivity (mS/cm)	1.33	24.46	149.80	2.22
TDS (ppm)	667	12,550	74,900	1,112
Salinity (PSU)	0.67	15.25	70.00	1.15

Table 2: Taxonomic species list of aquatic micro-invertebrates for four sampling sites in the lower Nata River, collected in August 2012 at low water levels. Rotifera were classified according to the system followed by Brain (2002) and Segers (2008).
(+) = present, (-) = absent

Class	Order	Species	Nata1	Nata2	Nata3	Nata4
Maxillopoda	Calanoida	*Metadiaptomus transvaalensis* Methuen, 1910	+	-	-	+
Maxillopoda	Cyclopoida	*Eucyclops sublaevis* (Sars, 1927)	+	-	-	+
Branchiopoda	Cladocera	*Moina belli* Gurney, 1904	-	+	-	-
Branchiopoda	Cladocera	*Moina micrura* Kurz, 1874	+	-	-	+
Monogononta	Ploima	*Asplanchna brightwelli* Gosse, 1850	+	-	-	-
Monogononta	Ploima	*Brachionus caudatus austrogenitus* Ahlstrom, 1940	+	-	-	+
Monogononta	Ploima	*Brachionus calyciflorus* Pallas, 1766	+	-	-	+
Monogononta	Ploima	*Brachionus falcatus* Zacharias, 1898	+	-	-	-
Monogononta	Flosculariaceae	*Conochilus coenobasis* (Skorikov, 1914)	+	-	-	-
Monogononta	Flosculariaceae	*Filinia longiseta* (Ehrenberg, 1834)	+	-	-	+
Monogononta	Flosculariaceae	*Filinia opoliensis* (Zacharias, 1898)	+	-	-	+
Monogononta	Ploima	*Keratella tropica* (Apstein, 1907)	+	-	-	+
Monogononta	Ploima	*Lecane papuana* (Murray, 1913)	+	-	-	+

Digononta	Bdelloidea	*Rotaria neptunia* Ehrenberg, 1832	+	-	-	+

Table 3: Taxonomic species list of aquatic micro-invertebrates for the lower Nata River and Makgadikgadi Pans. Data for the Nata River is from the present paper, while that for the Makgadikgadi Pans was compiled from Seaman et al. (1991) and McCulloch et al. (2008). (+) = present, (-) = absent/identified.

Taxon	Present Study (Lower Nata River, Nata Village)	McCulloch et al. 2008 (Sua Pan, Makgadikgadi)	Seaman et al. 1991* (Makgadikgadi Pans)
Anostraca			
Branchinella ornata Daday, 1910	-	+	+
Branchinella spinosa (Milne-Edwards, 1840)	-	+	+
Conchostraca			
Leptestheria striatoconcha Barnard, 1924	-	+	+
Cladocera			
Daphnia barbata (Weltner, 1897)	-	+	+
Moina belli Gurney, 1904	+	+	-
Moina micrura Kurz, 1874	+	-	-
Moina macrocopa (Strauss, 1820)	-	-	+
Copepoda			
Lovenula africana (Daday, 1908)	-	+	+
Metadiaptomus transvaalensis Methuen, 1910	+	+	+
Eucyclops sublaevis (Sars 1927)	+	-	-
Mesocyclops leuckarti (Claus, 1857)	-	-	+
Ostracoda			
Limnocythere tudoranceai Martins, 1990	-	+	-
Potamocypris Brady, 1870 sp.	-	+	-
Plesiocypridopsis aldabrae (Muller, 1898)	-	+	-
Sclerocypris exserta makarikarensis	-	+	+

Martins, 1988			
Rotifera			
Asplanchna brightwelli Gosse, 1850	+	-	-
Brachionus caudatus austrogenitus Ahlstrom, 1940	+	-	-
Brachionus calyciflorus Pallas, 1766	+	-	-
Brachionus falcatus Zacharias, 1898	+	-	-
Conochilus coenobasis (Skorikov, 1914)	+	-	-
Filinia longiseta (Ehrenberg, 1834)	+	-	-
Filinia opoliensis (Zacharias, 1898)	+	-	-
Keratella tropica (Apstein, 1907)	+	-	-
Lecane papuana (Murray, 1913)	+	-	-
Rotaria neptunia Ehrenberg, 1832	+	-	-

*Data is that of Eccles (undated) based on samples collected in 1957.

TRICHODINA DIAPTOMI (CILIOPHORA: PERITRICHIA) FROM TWO CALANOID COPEPODS FROM BOTSWANA AND SOUTH AFRICA, WITH NOTES ON ITS LIFE HISTORY

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SUMMARY

Members of the genus *Trichodina* are mostly found on fish, but have also been recorded from a variety of other aquatic organisms, including calanoid copepods. So far, it appears that all the trichodinid populations collected from calanoids in various parts of the world are the same species, i.e. *Trichodina diaptomi* Šrámek-Hušek, 1953. This paper reports on a new record for *T. diaptomi* from *Metadiaptomus meridianus* in a large reservoir in South Africa, as well as on a new host species, *Metadiaptomus transvaalensis*, and a new record from pools in an ephemeral river in northern Botswana, therefore adding a new country to the distribution of this species. We used the history of the discovery of *T. diaptomi* in different parts of the world and came to the conclusion that it is a cosmopolitan species, exclusively associated with copepods of the order Calanoida. Based on existing information, *T. diaptomi* does not appear to have a reservoir host. Against this background, we provide a discussion on the possibility that, although no dormant stage has been recorded for any trichodinid, it may be possible that *T. diaptomi* possesses some form of diapause and that this might be related to that of calanoid copepods.

Key words: ephemeral habitat, *Metadiaptomus meridianus, Metadiaptomus transvaalensis*, trichodinid, survival strategies.

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INTRODUCTION

Members of the genus *Trichodina* Ehrenberg 1830 of the order Mobilida are epibionts or ectoparasites represented by more than 200 species (Silva-Briano *et al.* 2011). Most species are associated with freshwater fish, but a number have been described from amphibians, a coelenterate, molluscs, sponges, tunicates, hydrozoans and marine piscean hosts (Basson & Van As 2006). On a number of occasions trichodinids have been found associated with different species of freshwater planktonic copepods in the former Soviet Union (Dogiel 1940), the former Czechoslovakia (Šrámek-Hušek 1953; Lom 1960a), China (Chen 1963), Poland (Migala & Grygierek 1972), South Africa (Basson & Van As 1991), Australia (Green & Shiel 2000), India (Asmat 2004), Brazil (Da Silva *et al.* 2009) and Mexico (Silva-Briano *et al.* 2011).

Copepods form critical components of the world's aquatic ecosystems and are cornerstones in aquatic food webs. These secondary producers consume micro-organisms and serve as primary prey for early life-history stages of many economically important fish, amongst others (Bron *et al.* 2011). Dormancy is one of the life-history characters of freshwater zooplankton that is affected by environmental factors. The term dormancy encompasses both diapause and quiescence and in the order Calanoida the typical dormant stages are diapausing eggs that differ from subitaneous eggs in the structure of the envelope (Gyllström & Hansson 2004). The trichodinid association with Copepoda of the order Calanoida makes for an interesting story and opens up many questions concerning trichodinid life history.

The present record is the first of a mobiline trichodinid on calanoid copepods in Botswana, as well as the first record of *Metadiaptomus transvaalensis* Methuen, 1910 as host species. The aim of this study is to confirm that trichodinids collected from calanoid copepods in the Nata River in north-eastern Botswana are in fact *T. diaptomi* Šrámek-Hušek, 1953 and to record a new host species for this ciliophoran. A discussion on the life-history stages of trichodinids is provided, following the discovery on copepods that are capable of forming dormant stages in this seasonal and highly unpredictable river.

A second record of *T. diaptomi* from *M. meridianus* (Douwe, 1912) in the Free State, South Africa, is also provided. Morphometric data of both populations are provided.

MATERIALS AND METHODS

During a long-term qualitative survey aimed at determining the diversity and distribution of zooplankton of the rivers, lakes and wetlands of northern Botswana, zooplankton was sampled from a variety of habitats using a plankton net of 50 µm mesh size. Samples collected from the Nata River (Fig. 1A) (S 20°12.290' E 026°11.302') on 15 and 16 August 2012 (late-winter) contained the calanoid copepod *Metadiaptomus transvaalensis*. On 20 and 21 November 2012 (late spring) plankton was collected during a fish and plankton survey at Rustfontein Dam in the Free State Province, South Africa that contained *M. meridianus*. These copepod species were infested with a mobiline trichodinid of the genus *Trichodina*. Live observations were made in a temporary field laboratory using both a Nikon Eclipse E100 and a Nikon SMZ800 light microscope and micrographs taken using a Nikon DS-Fi1 camera attached to both the compound and dissecting microscopes. Thereafter, infested calanoids were placed on slides and air-dried. In the laboratory in Bloemfontein, air-dried smears were impregnated with silver nitrate using a modified version of Klein’s technique, proposed by Lom (1958) and described by Wellborn (1967), in order to study details of the adhesive disc using a Zeiss Axiophot compound microscope and photos taken with a Zeiss AxioCam ICc 5 camera. All measurements were made using Zen 2012 SP2 Software, are presented in micrometres and follow the uniform specific characteristic system described by Lom (1958). Denticle descriptions are based on the method provided by Van As and Basson (1989). Minimum and maximum values are given, followed in parentheses by the arithmetic mean, standard deviation and number of specimens measured. In the case of the number of denticles and number of radial pins, the mode is provided instead of the arithmetic mean. Body diameter is measured as the adhesive disc plus border membrane.

Physical water quality parameters (temperature, pH, dissolved oxygen concentration, conductivity, total dissolved solids and salinity) were measured on site using a Hanna HI 9828 Multiparameter.

COLLECTION LOCALITIES

Nata River, Botswana

The Nata River is a sandy-bedded seasonal river which originates in the Zimbabwe Plateau just beyond the eastern margin of the Kalahari Desert and ends in the low lying depression comprising the Makgadikgadi Pans in north-eastern Botswana. It has a mean annual flow of 279 million m^3. The climate in the Nata River region is semi-arid, with low, unpredictable rainfall and high evaporation rates. Flow is erratic and during some years it flows for an extended period, while it may not flow at all for several years during periods of drought (Hitchcock & Nangati 2000; Hitchcock 2003). Peak flow in the Nata River is between January and March (Hitchcock 1995) and when the river begins to dry, water is retained in the riverbed in a number of large pools (Friederich & Gould 1986).

Rustfontein Dam, South Africa (Fig. 1B)

Rustfontein Dam is fed by the Upper Modder River that is a tributary of the Orange-Vaal River System, drains an area of 7 960 km^2 and has a mean annual runoff of 184 million m^3 (Koning & Roos 1999; Koning *et al.* 2000).

RESULTS

TRICHODINA SPECIES – NATA POPULATION (Figs. 2A - D, 4A & B)

Host and locality: *Metadiaptomus transvaalensis*, Nata River (S 20°12.290' E 026°11.302'), Nata, Botswana.

Site: Carapace (Figs 3A-E).

Reference material: Slides 2012/08/16-48 and 2012/08/16-79 in the collection of the Aquatic Ecology Laboratory, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

Description: Medium-sized trichodinid with flattened, disc-shaped body. Body dimensions are presented in Table 1. Centre of adhesive disc shows a clear circle. Denticles are tightly packed with small spaces between them.

Nuclear apparatus consists of a large C-shaped macronucleus, very constant in shape. In some specimens (just more than 50% of measured specimens) small oval micronucleus visible in +y position, sometimes lying in clear indentation of macronucleus (see Table 1).

Denticle description: Blade strongly developed, filling large part of area between y-axes. Distal surface slightly rounded, higher than tangent point. Posterior margin forming semi-lunar curve with deepest point at same level as apex. Apex pointed, almost touching y+1 axis in some specimens, while extending slightly beyond y+1 axis in others (Figs. 4A & B). Blade apophysis prominent in all denticles. Section connecting blade and central part relatively delicate. Central part robust, tapering to a sharply rounded point in some specimens, but more rounded in others. Central part not loosely connected to previous denticle. Central part extends more than halfway to y-axis. Section above x axis triangular, whilst section below x axis parallel for half the distance, then slanting away towards ray. In some denticles central part shows slight indentation corresponding to ray apophysis. Apophysis of ray strongly developed in most denticles. Central part connecting ray strongly developed. Ray strongly developed, of same thickness throughout length with a rounded point in some denticles and sharper in others. Rays parallel to y-axes in some specimens, while slightly curved towards y+1 axis in some denticles. Rays almost touching central circle in most denticles. Ratio of section below and above x axis just less than 1 (0.8-0.9). Central circle's border (periphery) well defined, but does not always impregnate in same way in all specimens. Central circle mostly only slightly granular in appearance with uneven wavy border in some.

***TRICHODINA* SPECIES - RUSTFONTEIN POPULATION** (Figs. 2E & F)

Host and locality: *Metadiaptomus meridianus*, Rustfontein Dam (S 29°16.246' E 026°36.366'), Free State Province, South Africa.

Site: Carapace.

Reference material: Slides 2012/11/30-16 and 2012/11/30-17 in the collection of the Aquatic Ecology Laboratory, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

Description: Measurements for this population are included in Table 1.

Denticle description: Similar to previous population.

Remarks: These two trichodinid populations without doubt both belong to the same species, i.e. *T. diaptomi*. The *T. diaptomi* population from Rustfontein Dam is very similar in overall body dimensions to the population described by Basson and Van As (1991) from Bloemfontein. Both these populations were not only collected from the same host, i.e. *M. meridianus*, but also during the the warmer months, i.e. late spring and early summer months (from Rustfontein Dam and Bloemfontein respectively). This could explain the similarities in the dimensions of these two populations. *Trichodina diaptomi* from the Nata River (Botswana), collected at much lower water temperatures during late winter (see Table 2), as well as from a new host record (*M. transvaalensis*), shows overall body dimensions that are larger than those from *M. meridianus*. The occurrence of larger winter specimens corresponds with findings of other authors such as Kazubksi and Migala (1967; 1968) and therefore the larger Nata River population is most likely due to the fact that these specimens were collected in the winter when the water temperature was an average of 17.5ºC, compared to a temperature of 23.2ºC measured at Rustfontein during late spring (See Table 2). The population of *T. diaptomi* from Australia from *B. fluvialis* as presented by Green and Shiel (2000) also concurs with that from *M. transvaalensis* in overall body dimensions. Some small differences were found in the mean body and adhesive disc diameters between the two South African populations and the Australian population, also collected during spring, with the latter being slightly larger. These differences could be due to the fact that the trichodinids were found on a completely different host species. Furthermore, the Australian population was collected and then kept at an ambient temperature of 20ºC that was lower than the water temp the South African populations were collected at. The latter is most likely a more plausible explanation. The only population that does not agree with the dimensions of *T. diaptomi* is the population provided by Asmat (2004). This author described a trichodinid he identified as *T. diaptomi* from two fish species. This trichodinid very likely represents *Trichodina acuta* Lom 1961, not *T. diaptomi* as the latter species has never before been reported from fish. Furthermore, the much large body dimensions (see Table 1) fall well within the range of the well-known fish trichodinid *T. acuta*.

WATER QUALITY

Several standard physical water parameters such as temperature, pH, dissolved oxygen concentration, conductivity, total dissolved solids and salinity were measured for both localities (see Table 2). While *T. diaptomi* is considered to be a freshwater species, this study clearly shows the wide tolerance it has for various water parameters, specifically water conductivity, TDS and salinity as it was found in water with low values for these three parameters (284 μS/cm, 142 ppm and 0.13 PSU respectively at Rustfontein Dam) to parameters averaging 1334 μS/cm, 667 ppm and 0.67 PSU respectively in the Nata River. In no other study to date has any reference been made to the water quality parameters and therefore no indication of the ability of this trichodinid species to occur and survive an array of environmental conditions.

DISCUSSION

The characteristics and measurements of both the Nata and Rustfontein populations are practically identical to the population described from the Free State, South Africa, by Basson and Van As (1991) although the Nata population is slightly larger as discussed above. There is no doubt that this is the same species, i.e. *Trichodina diaptomi.* As mentioned previously, a trichodinid has been reported from several calanoid hosts in various locations worldwide. A comparison of the characteristics and measurements of all the previously documented populations (some summarised in Basson & Van As 1991 and the rest in Table 1) from calanoids indicates that these are all the same species, i.e. *Trichodina diaptomi*. It is interesting that this species, associated with members of the order Calanoida is so widely distributed all over the world. This raises questions on its host specificity and method of dispersion that requires a revisit to previous reports on its discovery from different parts of the world.

Dogiel (1940) first described a trichodinid from the body surface of a *Diaptomus* species in the former Soviet Union (USSR), which he named *Trichodina domerguei* f. *megamicronucleata* and reported that the population of trichodinids he collected from a goldfish was the same species (Lom 1960a; Basson & Van As 1991; Green & Shiel 2000).

Initially trichodinids were not stained with silver nitrate and many species were mistakenly considered to be the same. Some trichodinid species were identified as different forms and/or subspecies of *Trichodina domerguei*, some of which displayed similar characteristics (such as the central circle) to that of the calanoid trichodinid, hence the name given to the latter by Dogiel (1940).

The next report was that of Šrámek-Hušek (1953) who described a new form, i.e. *Trichodina domerguei* var. *diaptomi* Šrámek-Hušek, 1953 from *Diaptomus vulgaris* from the former–Czechoslovakia. (Lom 1960a; Basson & Van As 1991; Green & Shiel 2000). Up until this point no photomicrographs had been presented, making it difficult for later authors to know exactly what Dogiel (1940) and Šrámek-Hušek (1953) were dealing with.

In 1960, Lom (1960a) included photomicrographs of silver impregnated adhesive discs of a trichodinid he collected from *Diaptomus vulgaris*, *Diaptomus castor* and *Eudiaptomus gracilis*, also from the former Czechoslovakia (Basson & Van As 1991; Green & Shiel 2000). Lom (1960a) concluded that the trichodinids from goldfish and those from calanoids were two different species based on dimensions and transmission experiments. He split Dogiel's (1940) material into two groups and suggested that the trichodinids from goldfish are representatives of *Trichodina reticulata* Hirschmann and Partsch, 1955 and that those from calanoids be assigned to *Trichodina domerguei* f. *latispina* Dogiel 1940.

The next report of a calanoid trichodinid originated from Mainland China when Chen (1963) reported it from various fish and tadpole species, as well as the calanoids *Sinodiaptomus sarsi* and *Neodiaptomus handeli*. He followed Lom (1960a) in also identifying it as *T. domerguei* f. *latispina*, as well as conducting cross-infestation experiments. Chen (1963) reportedly succeeded in transferring this trichodinid from calanoids to different carp species, but did not manage to transfer known fish trichodinids (*T. reticulata*, *T. nobilis* Chen, 1963 and *T. nigra* Lom, 1961) to the copepods (Basson and Van As 1991).

In 1964 trichodinids of calanoids were placed into a separate subspecies for the first time by Haider (1964) in his comprehensive monograph on trichodinids when he named them *T. domerguei* subsp. *megamicronucleata* Dogiel, 1940. He also then synonymised *T. domerguei* f. *diaptomi* with *T. domerguei* f. *megamicronucleata* (Basson & Van As 1991). Almost a decade later *T. domerguei* subsp. *megamicronucleata* was found on an unidentified *Diaptomus* species and *Eudiaptomus zachariasi* from Poland by Migala and Grygierek (1972).

Finally, 19 years later, Basson and Van As (1991) provided a full taxanomic description of this ciliophoran based on material collected from *Metadiaptomus meridianus* in Bloemfontein, South Africa. Basson and Van As (1991) reviewed all the previous records and concluded that they all represented the same widely distributed trichodinid and named it *Trichodina diaptomi*. Similar to Lom (1960a) they concluded that fish do not provide a suitable substrate for *T. diaptomi* to establish a viable population.

During plankton surveys in 1991, 1992 and 1995 in billabongs of the Murray River, Australia, Green and Shiel (2000) collected calanoid trichodinids that they identified as *Trichodina diaptomi* as described by Basson and Van As (1991) as it corresponded closely with the description provided by these and earlier authors. Three calanoid species were collected, namely *Boeckella fluvialis*, *Boeckella minuta* and *Calamoecia lucasi*. Trichodinids, however, were only present on the former two and only on adults and copepodites of a certain size. Green and Shiel (2000) suggested that one explanation might be that these trichodinids only occur on copepods and copepodites of large species. This would also explain their absence from *Calamoecia lucasi,* the adults of which are smaller in size than the infested copepodites of the two larger species.

The next report of *T. diaptomi* is worthy of note as Asmat (2004) claims to have collected *T. diaptomi* from the gills of two freshwater fishes, *Tetraodon cutcutia* and *Gagata cenia*, from West Bengal, India in 1996.

This was followed by collections of *T. diaptomi* from a South American calanoid *Notodiaptomus deitersi* in 2006 and 2007 in Brazil (Da Silva *et al.* 2009).

The most recent report on *T. diaptomi* was published in 2011 by Silva-Briano *et al.* (2011) after they collected it from *Mastigodiaptomus albuquerquensis* and *Mastigodiaptomus montezumae* in the north-central region of Mexico.

We believe all the trichodinid populations so far described from calanoids represent the same species, namely *T. diaptomi*, with the exception of that of Chen (1963). His description of *T. domerguei* f. *latispina* from fish, calanoids and tadpoles most likely represents more than one trichodinid species. He did not employ silver impregnation, making it impossible to come to a conclusion concerning the trichodinids from fish and tadpoles. However, since his population measurements show such a wide range and the lower range falls well within that for *T.* d*iaptomi*, we suspect that he probably did encounter this species on calanoid copepods. The upper range, however, coincides with the ranges of various trichodinids found on fish. It could be that he had a mixed population of *T. diaptomi* as well as fish trichodinids, but mistakenly took it to be a single species. Workers such as Lom (1960a) and Basson & Van As (1991) could not succeed in forming viable populations of *T. diaptomi* on any fish species; therefore the trichodinids Chen (1963) observed from calanoids were in all probability *T. diaptomi*, while those from fish and tadpoles were not.

The other doubtful record of *T. diaptomi* is that of Asmat (2004) in which he described a trichodinid he identified as *T. diaptomi* from two fish species. His morphometric dimensions are far above that of the other *T. diaptomi* populations, but fall well within the range of *Trichodina acuta* that is a well-known trichodinid of fish and also possesses a central circle. He makes no reference to ever finding trichodinids from a calanoid. Furthermore he provided a micrograph of the alleged *T. diaptomi*, which shows clear similarities with the cosmopolitan *T. acuta*.

Presently the known worldwide distribution of *T. diaptomi*, associated with calanoids, includes the former Soviet Union (Dogiel 1940), the former Czechoslovakia (Šrámek-Hušek 1953; Lom 1960a), China (Chen 1963), Poland (Migala & Grygierek 1972), South Africa (Basson & Van As 1991; present study), Australia (Green & Shiel 2000), Brazil (Da Silva *et al.* 2009), Mexico (Silva-Briano *et al.* 2011) and Botswana (present study). Some authors (Da Silva *et al.* 2009; Silva-Briano *et al.* 2011) expressed their uncertainty as to the origin of the occurrence of *T. diaptomi* in specific parts of the world and whether it was introduced or occurs there naturally.

We believe *T. diaptomi* to be a cosmopolitan species naturally associated with calanoid hosts exclusively. The present study was a joint survey of zooplankton and fish parasites and despite the sampling of all trichodinids from fish from the same pools in the Nata River, *T. diaptomi* was never collected from any fish species. We believe fish are not reservoir hosts for these ciliophorans, which raises the important question on how these trichodinids survive when populations of calanoids decline or temporarily disappear from a water body in response to harsh environmental conditions caused by abiotic or biotic factors.

Green and Shiel (2000) observed that *T. diaptomi* only occurred during October and November, despite the calanoids being present year round, but did not provide potential reasons for the absence of trichodinids during the rest of the year. If

T. diaptomi does not have a reservoir host and cannot form viable infestations on fish, the question involuntarily arises as to where they go for the other 10 months of the year? The answer to this question has never been addressed by any workers, as most merely recorded and described the trichodinid they encountered on calanoids. We believe that in order to provide a feasible hypothesis for this, one will have to have a look at the hosts in this particular case, especially since *T. diaptomi* was reported for the first time from a habitat that was rapidly drying up, in a system where this is a natural and regular occurrence.

Zooplankton was only sampled on one occasion in November from Rustfontein Dam, so it was not possible to observe whether the trichodinid population fluctuated or even disappeared at times. However, Green and Shiel (2000) sampled plankton year round in 1991, and they observed that despite the fact that calanoids were present from January to early December, they only harboured trichodinids in October and November (spring). Interestingly, these calanoids formed a major component of the zooplankton from May (late autumn) to early November, until their percentage abundance declined sharply in early October. They experienced a brief recovery in late October and then remained low for the rest of the year. Simultaneously, the trichodinid infestations peaked in early October, declined during the copepod resurgence and peaked again when the copepod abundance declined in late November. Green and Shiel (2000) suggested that this may either indicate that the infestation contributed to the copepod decline or that the trichodinids were able to establish when the copepod population was declining for other reasons such as poor nutrition or environmental factors.

While seasonality was not investigated during the present study, trichodinids were common on their hosts during mid-winter (July) in Botswana, as well as in early summer in South Africa, both in Rusfontein Dam (the present study) and Bloemfontein (Basson and Van As 1991). The occurrence of *T. diaptomi* during mid-winter in Botswana differs with the findings of Green and Shiel (2000) who found trichodinids only in October and November (summer) in their study.

Although sampling in the Nata River took place in August only, we do know that it is an ephemeral river that dries up annually. Since peak flow in this system takes place between January and March, the last pools in which we sampled would have dried up before the next flood, which, for the organisms of such aquatic environments, is a catastrophic event.

Natural zooplankton population densities and dynamics fluctuate seasonally and annually in response to their abiotic environment, including catastrophic events such as drying, as well as to biotic factors. Adaptive responses to these factors can be expressed as morphological, behavioural or life history changes. Of the latter responses dormancy is one of the most evident and may be viewed as an escape in time, which may range from days to hundreds of years (Dahms 1995).

In temporary habitats that dry seasonally, such as the Nata River, the advantage of dormancy is quite obvious, but it is also extremely important in large permanent water bodies (Gyllström & Hansson 2004) such as Rustfontein Dam and most probably also the billabongs of the River Murray in Australia. This is because environmental variables in permanent water bodies also fluctuate temporarily. The question arising from the drying event in the Nata River is this: zooplankton, such as calanoids, possess a life history adaptation, which most probably evolved a long time ago, but what do the trichodinids do to survive such an event? According to Mueller (1938) and Lom (1960b) no cyst or dormant stage is known for the genus *Trichodina*, and none has ever been recorded by any worker. Against the background of the narrative of *T. diaptomi*, it appears that not only does this cosmopolitan trichodinid successfully occur on hosts that are not available year round, but it also appears to be able to somehow survive catastrophic events such as the complete desiccation of their aquatic habitat and consequent disappearance of their hosts, sometimes for extended periods. We would therefore like to postulate that some form of dormant stage probably exists for *T. diaptomi* and that it may be linked to the diapause of the calanoids in the case of this trichodinid species specifically.

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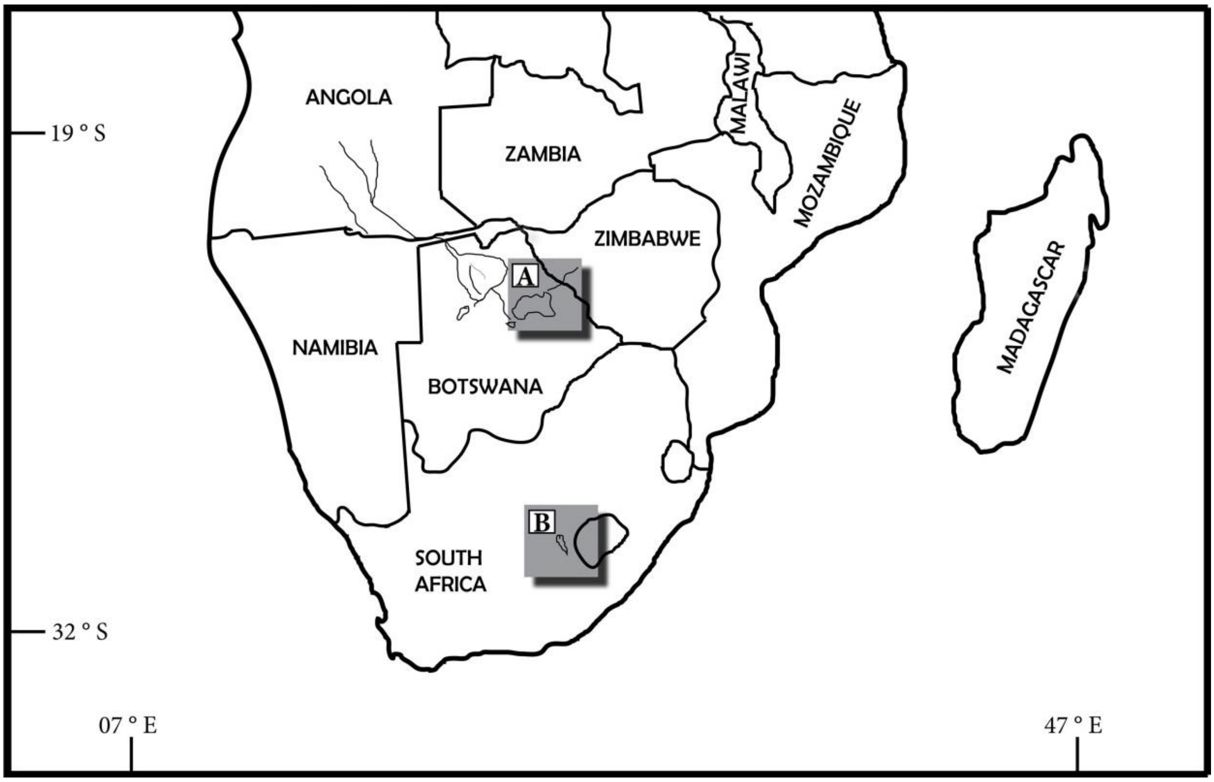
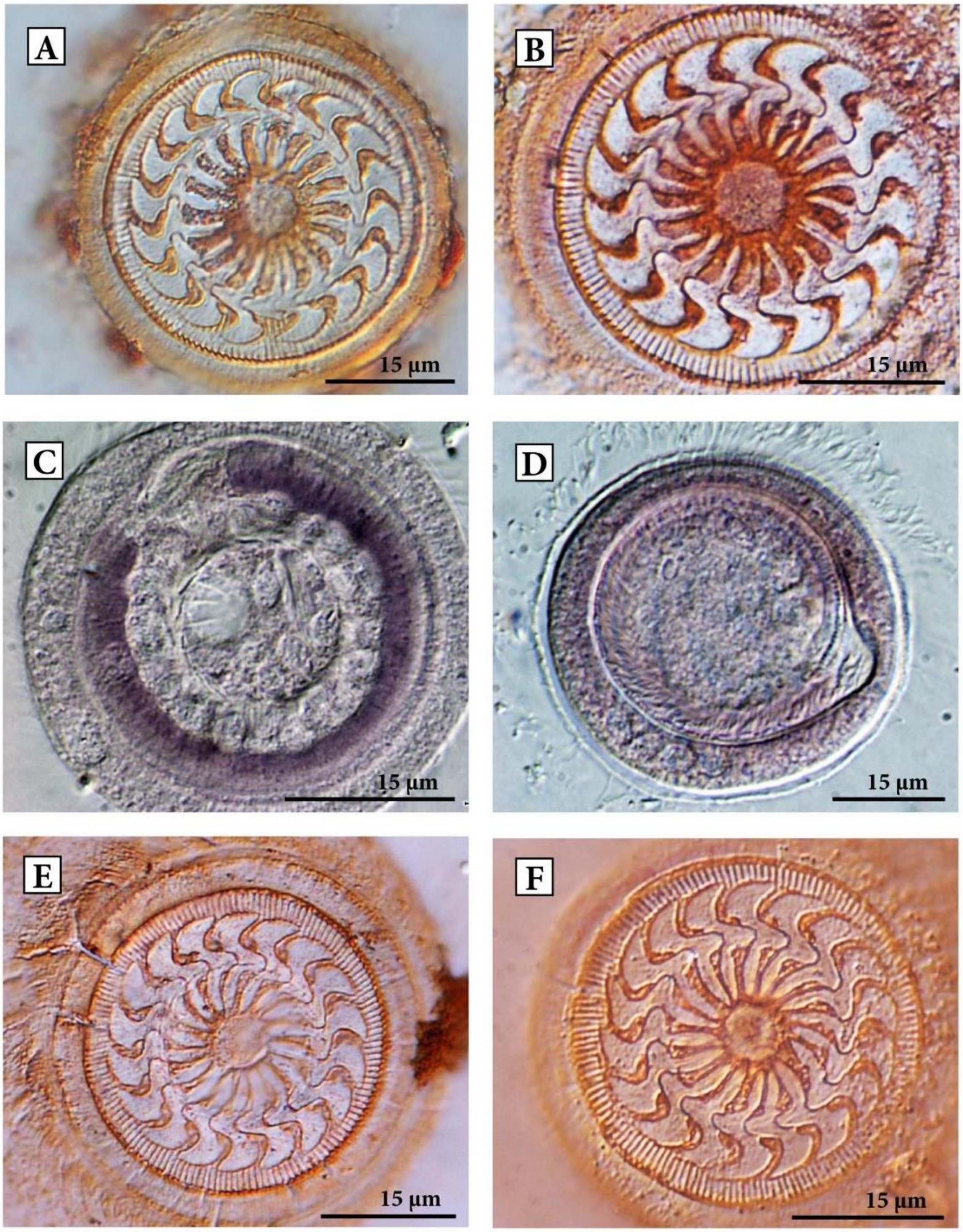
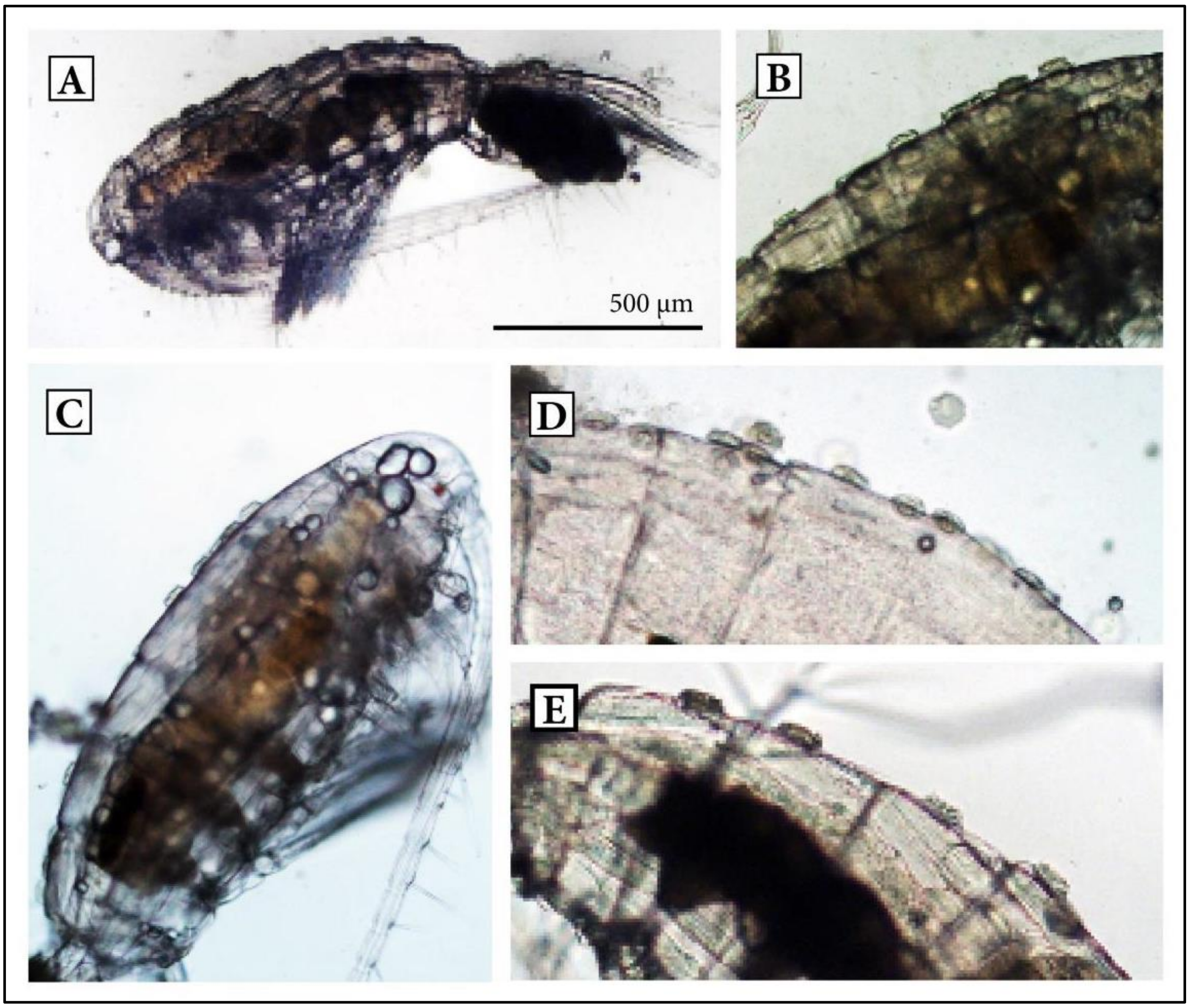


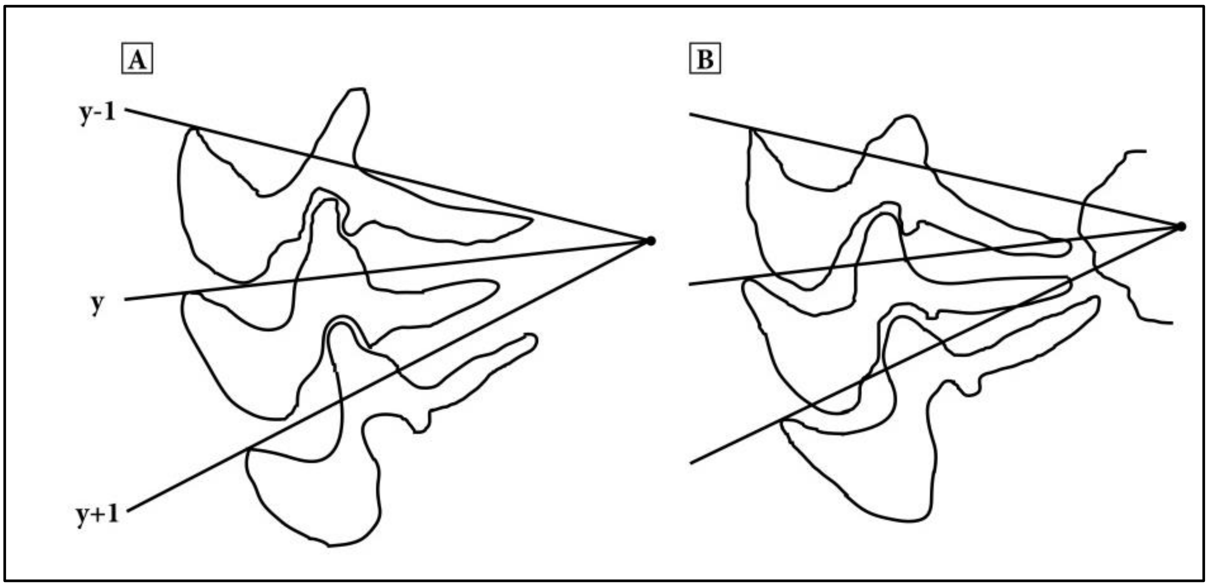
Fig. 1. Map of southern Africa indicating the two localities where *Trichodina diaptomi* Šrámek-Hušek, 1953 were collected from the carapace of *Metadiaptomus transvaalensis* (A) and *M. meridianus* (B) respectively. A. Nata River in Botswana. B. Rustfontein Dam in South Africa.



Figs. 2 A-F. Micrographs of silver impregnated adhesive discs (A, B, E & F) and haematoxylin stained specimens (C & D), showing the nuclear apparatus (C) and adoral spiral (D) of *Trichodina diaptomi* Šrámek-Hušek, 1953 from the Nata River (A-D) and Rustfontein Dam (E & F).



Figs. 3 A-E. Micrographs of *Metadiaptomus transvaalensis* with *Trichodina diaptomi* Šrámek-Hušek, 1953 on the carapace collected from the Nata River, Botswana in August 2012.



Figs. 4 A&B. Diagrammatic drawings of the denticles of *Trichodina diaptomi* Šrámek-Hušek, 1953 from the carapace of *Metadiaptomus transvaalensis* from the Nata River, Botswana.

Table 1. Biometrical data (in µm) of different populations of *Trichodina diaptomi* Šrámek-Hušek, 1953

Trichodinid Species	*T. diaptomi*	*T. diaptomi*	Not *T. diaptomi*, probably *T. acuta*	*T. diaptomi*	*T. diaptomi*	*T. diaptomi*	*T. diaptomi*
Host	*Metadiaptomus meridianus*	*Boeckella fluvialis*	*Tetraodon cutcutia*	*Notodiaptomus deitersi*	*M. albuquerquensis*	*M. transvaalensis*	*Metadiaptomus meridianus*
Locality	South Africa	Australia	India	Brazil	Mexico	Botswana	South Africa
Reference	Basson & Van As (1991)	Green & Shiel (2000)	Asmat (2004)	Da Silva *et al.* (2009)	Silva-Briano *et al.* (2011)	Present study	Present study
Body Diam	33.8-48.7(41.5)	35.3-49.6 (43.6)	40.8-55.5 (50.1)	(38.3 ±4.2)	38.1-44.6 (40.4)	40.3-53.7 (45.9 ±2.9)	37.1-45.9 (41.3 ±2.2)
Adh disc diam	27.9-39.9 (33.8)	30.2-42.6 (35.9)	32.6-46.6 (41.4)	(31.5 ±3.1)	29.3-39.8 (34.5)	31.9-43.5 (36.9 ±2.5)	28.3-38.8 (33.1 ±2.3)
B.m.w.	2.6-5.4 (4.0)	1.8-4.8 (3.6)	3.6-5.1 (4.3)	-	2.6-3.8 (3.0)	3.5-4.9 (4.3 ±0.3)	3.4-5.1 (4.1 ±0.4)
Dent ring diam	14.8-22.6 (19.6)	14.7-39.1 (20.1)	18.3-26.5 (23.4)	-	18.1-22.8 (19.8)	16.3-24.6 (21.1 ±1.9)	15.0-20.2 (18.1 ±1.4)

C.c.d.	4.4-7.9 (5.9)	-	7.1-9.2 (8.0)	-		5.2-9 (6.8 ±0.9)	3.7-6.3 (5.0 ±0.6)
Dent number	15-20 (18)	15-19 (17)	18-25 (-)	18-20 (19)	20-24 (22)	17-21 (18)	16-22 (18)
Rad p/dent	7-11 (9)	5-9 (9)	7-10 (-)	8-10 (-)	8-11 (9)	8-10 (9)	8-11 (10)
Dent length	4.8-7.7 (6.2)	4.4-7.6 (6.2)	5.6-8.2 (6.4)	-	5.7-6.9 (6.3)	5.2-7.4(6.3 ±0.6)	4.1-7.2 (5.5 ±0.6)
Blade length	2.9-6.9 (3.8)	3.4-5.7 (4.4)	3.1-4.6 (3.9)	-		3.2-4.8 (4.2 ±0.4)	2.7-4.7 (3.5 ±0.4)
C.p.w.	1.4-2.7 (2.0)	1.2-2.9 (2.0)	2.0-3.6 (3.2)	-		1.9-3.1 (2.4 ±0.3)	1.6-2.7 (2.2 ±0.3)
Ray length	2.8-6.1 (4.4)	3.8-6.4 (4.9)	3.1-5.2 (4.1)	-	4.8-6.2 (5.72)	3.4-6.7 (5.0 ±0.6)	3.5-6.0 (4.6 ±0.6)
Denticle span	-	-	9.3-12.7 (11.3)	-		9.8-12.9 (11.4 ±0.8)	9.2-12.5 (10.4 ±0.8)
Ma - shape	C	C	-	C	C	C	C

Ma - ext diam	32.3-50.2 (38.3)	29.1-42.0 (35.1)	-	-	26.5-39.2 (30.6 ±3.3)	25.7-38.7 (32.7 ±3.4)
Ma - thickness	4.1-10.2 (6.4)	6.8-13.4 (10.4)	-	-	3.6-6.2 (4.8 ±0.8)	3.5-7.3 (5.0 ±1.0)
Ma - x value	7.6-19.1 (12.6)	5.2-18.3 (11.8)	-	-	5.8-14.4 (9.0 ±2.5)	8.6-19.0 (12.2 ±2.3)
Mi - shape	oval	-	-	-	oval	oval
Mi - length	4.5-7.6 (5.8)	-	-	-	2.3-5.6 (3.6 ±1.0)	2.4-7.3 (4.1 ±1.3)
Mi - width	1.7-3.8 (2.8)	-	-	-	1.1-2.1 (1.5 ±0.3)	0.8-2.6 (1.9 ±0.4)
Mi - y position	+y	-	-	-	+y	+y
Mi- y value	7.0-26.8 (16.0)	-	-	-	0.9-17.8 (10.4 ±4.5)	3.1-18.5 (9.5 ±3.7)
Adoral spiral	400°	ca. 400°	390°	-	390-440°	395-410°

n1	27	50	20	10-20		30	34
n2	20	24	-	-		27	33
n3	9	-	-	-		12	24

Adh – adhesive, B.M.W. – Border membrane width, C.c.d. – Central circle diameter, C.p.w. – central part width, dent – denticle, Diam – diameter, ext – external, Ma – macronucleus, Mi – micronucleus, n1 – number of silver impregnated specimens measured, n2 – number of haematoxylin stained specimens measured for macronucleus, n3 – number of haematoxylin stained specimens measured for micronucleus, Rad p/dent – Radial pins per denticle.

Table 2. Physical water quality parameters measured in the Nata River and Rustfontein Dam during collection of infested metadiaptomids.

Location	Nata River	Rustfontein Dam
Date & Time	14/08/2012 at 10:45; 15/08/2012 at 12:50; 16/08/2012 at 09:12	20/11/2012 at 11:04
Temperature (°C)	15.37 – 19.19 (17.51)	23.32
pH	8.39 – 8.62 (8.54)	8.40
Dissolved oxygen concentration (%)	113.2 – 126.8 (119.72)	110.9
Conductivity(μS/cm)	1295 - 1374 (1334)	284
Total dissolved solids (TDS) (ppm)	647 – 687 (667)	142
Salinity (PSU)	0.65 – 0.69 (0.67)	0.13

Chapter 9

GENERAL DISCUSSION AND CONCLUDING REMARKS

GENERAL DISCUSSION

Fresh waters cover a mere 0.8% of the earth's surface, yet the more or less 125,000 freshwater species that have been described to date represent 9.5% of the known animal species on the planet. Hence, fresh waters as a whole may be considered biodiversity hotspots and their biodiversity may be much higher than these figures imply, considering that a large proportion of the global fresh waters are situated in recently glaciated regions, where there is low biodiversity and endemism (Strayer & Dudgeon 2010). Despite this, rivers and wetlands are almost certainly the most threatened of all ecosystems (Abellán *et al*. 2005), as biodiversity declines in these environments largely surpass that of the most endangered terrestrial ecosystems (Dudgeon *et al*. 2006). During the past century, humans' demands on freshwater ecosystems have increased dramatically, causing great anthropogenic biodiversity losses. The preservation of species richness and composition is vital as ecosystem function often depends on it (Strayer & Dudgeon 2010).

The most fragile of all freshwater systems are ephemeral (such as Lake Ngami, the Boteti River, Lake Xau and the Nata River) and endorheic (such as the Okavango River) systems (Seely *et al*. 2003) which are naturally situated in dryland areas. Human population growth in arid environments worldwide have led to greater pressure being placed on these systems, which are in a fragile state of hydrological and ecological balance (Seely *et al*. 2003). Many of these systems contain extensive wetlands. The Okavango Delta in the central Kalahari Desert, for example, is one of the world's largest and most unaltered wetlands which was listed as both a Ramsar site and a UNESCO World Heritage Site, in an effort to preserve it. This comes at a time when public attitudes towards wetlands have changed and the many benefits they provide to human society is recognised. Seely *et al*. (2003) pointed out that, amongst others, the services wetlands supply include freshwater and consumer products, carbon cycling, flood control, ecosystem sustainability, water purification, climate regulation and biodiversity maintenance services.

Many of these wetland values are linked to their biodiversity and yet the biodiversity of wetlands and other freshwater systems is poorly understood (Gopal & Junk 2000). Much research remains to be conducted in globally important wetlands such as the Okavango Delta and research is completely lacking in certain ephemeral water bodies such as Lake Ngami, the Boteti River, Lake Xau and the Nata River in the Kalahari Desert. In the case of the latter water bodies, the lack of research is mainly due to persistent drought which left a number of these systems dry for decades (see **Chapter 2**). The recent flooding of the water bodies associated with the Okavango Delta was due to consecutive years of record high floods in the catchment area in Angola. This has allowed an insight into the zooplankton species diversity of these aquatic ecosystems, as no such information was gathered prior to their drying. There is, therefore, no way to assess possible changes in species diversity brought about by prolonged drought and other factors, but documenting the zooplankton composition in these instant ecosystems has provided a snapshot of the species which play a vital role in creating the food webs. Such information will serve as background in assessing possible biological changes to the system, brought about by long term drought, amongst others.

ROTIFERA

The present study has pointed out that the rotifer species diversity (33 species) in the area as a whole is low from a global point of view, but not unusual for a water body in its geographical region. Segers (2008) mentioned that tropical Africa is notable for its relatively poor rotifer diversity and few endemics. Most of the rotifer species recorded from the study area are common and widely distributed. This correlates with the statements by Segers (2008) that many rotifer species are cosmopolitan and endemicity is centred in tropical South America and Australia. In their study on the rotifers of the Kgalagadi Transfrontier Park (formerly known as the Kalahari Gemsbok National Park), South Africa, Brain *et al*. (1995) also found that the rotifer diversity was very low. Hence, the low rotifer diversity in the Okavango Delta and its associated basins is not unusual for systems in the Kalahari Desert. It must, however, be kept in mind that sampling during the present study took place at a certain time of year only. The rotifer species diversity may, therefore, be much higher than results indicate. Despite this, the present study has added three new genera (*Asplanchnopus*, *Synchaeta* and *Synantherina*) and six new species (*Aspanchnopus multiceps*, *Epiphanes senta*, *Synchaeta pectinata*, *Conochilus dossuarius*, *Conochilus unicornis* and *Synantherina* sp.) to the list of rotifers from the waterways of northern Botswana.

Rotifers are particularly sensitive to water quality variations due to their high population turnover rates and display differences in tolerance to a number of biotic and abiotic parameters (Marneffe *et al*. 1998). Salinity is a dominant factor (Green 1993) and in subtropical climates, water temperature is likely to be a key factor in defining the community structure of rotifers, due to dramatic seasonal changes (Wen *et al*. 2011). *Brachionus, Lecane* and *Trichocerca*, for example, are known to be dominant in the tropics, while genera such as *Synchaeta* mostly occur in the cooler parts of the world, with an occasional species in the tropics (Wen *et al*. 2011), such as is the case with *Synchaeta pectinata* in the Okavango Delta. Furthermore, rotifer abundance and diversity is proportional to trophic status as it increases with an increase in eutrophication, but on the other hand decreases again when conditions become hyper-eutrophic (Green 1993; Wen *et al.* 2011). In slightly eutrophic environments, more food resources, such as algae, heterotrophic flagellates, bacteria, phytoplankton and small ciliates, are available for rotifers (Bonecker & Aoyagui 2005; Wen *et al*. 2011). Macro-filter-feeder rotifers, such as *Polyarthra*, *Synchaeta* and *Trichocerca,* mostly feed on edible algae, while bacteria-detritus particles and nanoplankton are consumed by micro-filter-feeders such as *Anuraeopsis fissa* and *Filinia longiseta* (Wen *et al*. 2011). The spatial and seasonal distribution of rotifers is also affected by variations in food supply (Bonecker & Aoyagui 2005). The species richness and abundance of rotifers can therefore serve as an indication of water quality and eutrophic state (Wen *et al*. 2011). The water of the Okavango Delta is not eutrophic which, in part, may also explain the low species diversity.

Two of the genera (*Aspanchnopus* and *Synchaeta*) and three of the species (*Asplanchnopus multiceps*, *Epiphanes senta* and *Synchaeta pectinata*), which were recorded in northern Botswana for the first time during the present study, were only collected from the water bodies that were inundated after being dry for decades (Figs. 5.2B, 5.10A and 5.13B). This indicates the importance of resting eggs and cryptobiosis (see **Chapter 3**) to the success and survival of members of the phylum Rotifera. Rotifers, and other micro-invertebrates, in temporary waters are adapted to a dual existence. They flourish when the water body is inundated, but being unable to actively migrate, have to adapt in other ways or rely on passive dispersal when water is absent. Monogonont and bdelloid rotifers have two different strategies for surviving desiccation. Bdelloid rotifers undergo a change in metabolism and enter into an anhydrobiotic state (Wallace & Snell 1991), while monogonont rotifers form diapausing embryos or resting eggs (Brain 2002) (see **Chapter 3**). Regardless of their strategy, they are able to repopulate the habitat when it is inundated again. De Stasio, Jr. (1990) stated that rotifer resting eggs may remain dormant for at least 35 years and dormant egg banks in the sediment have an important effect on the ecology and evolution of zooplankton species. They are critical in re-establishing rotifer communities after drought.

CLADOCERA

Forty five cladoceran species have been identified from the Okavango Delta (Ramberg *et al.* 2006) and although only 12 species were collected during the present study, it is important to note that this excludes the members of the family Chydoridae, which was the most diverse family. It also only encompasses species present at a certain time of year. cladoceran species diversity is also low from a global point of view, as other globally important wetlands, relatively similar to the Okavango Delta, host almost double the number of cladocerans species. For example, more than 80 species of cladocerans (Junk *et al.* 2006) have been identified from the Pantanal in South America.

Apart from the Chydoridae species which were collected at the majority of sampling sites, *Simocephalus vetulus* was the species most often encountered throughout the system, whereas *Ilyocryptus sordidus* was least often encountered and only present at three study sites in low numbers. *Macrothrix propinqua*, which was found across the entire study area, except in the Thamalakane River, was recorded from the Okavango Delta for the first time. A noteworthy feature is the relative absence of *Daphnia* from the system. Amongst the Daphniidae, *Daphnia* is the most speciose in South Africa (Seaman *et al.* 1999), yet in northern Botswana only one species of *Daphnia*, namely *Daphnia laevis* was present and it was only encountered in the panhandle, the Thaoge Channel and Lake Ngami.

Daphnia are limnetic (Seaman *et al*. 1999), live in the plankton (Siziba *et al*. 2011a) and are large-bodied cladocerans which most likely makes them very susceptible to predation by juvenile fish and small fish species. The limnetic zone is well-lit and free of aquatic vegetation, making it easy for predators to see their prey. A considerable proportion of the cladocerans within the system are littoral dwellers (such as Chydoridae, *Simocephalus* and *Macrothrix*) and those which occur in a variety of habitats (e.g. *Ceriodaphnia*), rather than planktonic. This points to the importance of predation in shaping the cladoceran communities within the water bodies of northern Botswana. *Daphnia laevis* was mostly encountered in 2011 when the floods were extremely high. At this time individuals displayed cyclomorphosis and had longer tail spines and hooded heads (see **Chapter 3**), which may have prevented predation by fish. In 2012 the species was only collected in the Thaoge Channel and did not display cyclomorphosis, most likely making them susceptible to predation. *Daphnia laevis* was not collected from the system in 2013.

All the cladoceran species and higher taxa (Chydoridae) sampled within the study area were present in the Okavango Panhandle at some stage or another during the study. This indicates the importance of the seasonally flooded floodplains in maintaining species diversity. As was the case with the rotifers, the floodplains which are more frequently inundated (Okavango Panhandle) displayed a higher species diversity than those which were dry for decades before being inundated. This is in accordance with the findings of a previous study (Siziba *et al.* 2012) in which it was found that the more frequently inundated areas in the Okavango Delta Fan had a higher species richness, diversity and abundance of viable micro-crustacean propagules in the sediment than the less frequently inundated areas.

COPEPODA

Previous records (Hart 1997; Hart *et al.* 2003; Siziba *et al*. 2011b) indicate that the genus *Tropodiaptomus*, subfamily Diaptominae, has been the only calanoid genus recorded from the Okavango Delta. During the present study, only *Tropodiaptomus schmeili* was collected from the Okavango Delta, as well as its associated basins. However, a possible new species of the genus *Metadiaptomus*, subfamily Paradiaptominae, was collected in the Okavango Panhandle and Lake Ngami during the present study. This is rather unusual as there are very few records of species of Paradiaptominae and Diaptominae co-occurring (Rayner 2000). Furthermore, while members of the genus *Tropodiaptomus* are generally associated with major drainage systems and inland lakes, species of *Metadiaptomus* are primarily confined to natural ephemeral and perennial pans, but may also be present in man-made lakes in semi-arid regions (Hart & Rayner 1994). The differences in habitat preference would explain why *Tropodiaptomus* is successful in the Okavango Delta and why *Metadiaptomus* was present in the ephemeral Nata River. The sudden presence of a possibly undescribed species of *Metadiaptomus* in the Okavango Delta is therefore thought-provoking.

Rayner and Heeg (1994) pointed out that most representatives of the southern African freshwater Diaptomidae have restricted distribution ranges, despite the fact that they may be passively dispersed. It is probable that they have restricted tolerance ranges for certain physical and chemical water quality parameters or that they require certain suitable niches, hence the lack of ability to colonise new water bodies (Rayner & Heeg 1994). Furthermore, there are vast areas of Africa which are yet to be covered in terms of diaptomid research. Rayner and Heeg (1994) pointed out that in southern Africa, there have been little or no collections of representatives of the family Diaptomidae in countries such as Angola, Zimbabwe, Zaire, Malawi and Mozambique. In short:

- Members of *Tropodiaptomus* and *Metadiaptomus* do not normally co-occur,
- *Metadiaptomus* is most likely to be found in ephemeral or perennial pans in semi-arid areas,
- Representatives of the family Diaptomidae have very limited distribution ranges,
- Members of the genus *Metadiaptomus* have not been recorded from the Okavango Delta before, and the species collected there during the present study may possibly be an undescribed species, and
- Angola, and other areas north of the delta, lack diaptomid research.

Could it be that the unusually high floods flushed ephemeral pans or wetlands along its course and that this species was washed into the delta from its natural habitat farther upstream? Should calanoids be collected in countries where no previous surveys have been conducted, it is likely that many new diaptomid species will be discovered. One African genus, for example, *Camerundiaptomus* Dumont & Chiambeng, 2002, is only known from the rainforests of Cameroon (Dumont & Chiambeng 2002) and has only recently been described. Furthermore, species such as *Metadiaptomus capensis* (Sars, 1907) and *Lovenula excellens* Kiefer, 1929 have only been collected from saline waters in localised areas of the Cape and Mpumalanga, South Africa, respectively (Rayner 2001).

A number of cyclopoid species were collected, but due to a lack of research on this group in southern Africa, identification is difficult. Members of the family Cyclopidae are successful predators in the Okavango Delta and its associated basins as they were present in all water bodies and at most study sites. This is not surprising as it is known that many members of this group of organisms are cosmopolitan (Boxshall & Defaye 2008) and occur in basically any type of aquatic habitat (Rayner 2001) (see **Chapter 3**).

WATER QUALITY AND HOW THE DELTA REMAINS FRESH

The occurrence and distribution of species as well as community structure in a particular water body is determined by habitat permanence and additional biotic and abiotic factors (Hart & Rayner 1994). There were no significant differences in abiotic factors such as physical water quality parameters between the different water bodies, with the exception of the Boteti River which had low oxygen concentrations, in 2012 only, and Lake Xau which showed an elevated conductivity, TDS and salinity compared to the rest of the water bodies included in the study area. Appendix 1 indicates the arithmetic mean values of the physical water quality parameters recorded throughout the study area during zooplankton surveys. In this appendix, results are separated for the Boteti River to indicate the dramatic differences in oxygen concentration between 2011 and 2012. Despite salinity, conductivity and TDS being elevated in Lake Xau, there were no species present in the lake that were not found in the other water bodies of northern Botswana, but the elevated salinity may have played a role in certain species being absent from Lake Xau, such as the calanoid copepod *Tropodiaptomus schmeili*. This water body is situated closer to the Makgadikgadi Pans (Fig. 2.4) and in hot and arid areas it is common that salt becomes concentrated in most wetlands (see **Chapter 2**). The Makgadikgadi and Etosha Pans are good examples of wetlands in the area in which salts have accumulated. The Okavango Delta is a unique exception to this, a characteristic it owes, in part, to its cyclic pulse flooding.

The Okavango Delta receives the bulk of its water as inflow from the Okavango River. Rainfall in the area of the Okavango Delta, which is only about 500 mm per year, occurs between November and March (Garstang *et al.* 1998; Ashton *et al.* 2003; Ross 2003, Kgathi *et al.* 2006) and provides only one third of the water in the delta. During the local rainy season, water levels do rise, but the flooding at this time is minor compared to the floods which emanate more than 1,000 km away. Rain falls in the tropical highlands of Angola between October and April (Mendelsohn & El Obeid 2004), more or less the same time as that in the Okavango Delta, but because of the slight gradient, water only reaches the northern tip of the panhandle by March or April. From this point, water is blocked by papyrus swamps and the gradient decreases even more resulting in the water taking on average four to five months to travel the length of the delta (about 250 km) (Mendelsohn & El Obeid 2004). While maximum flooding takes place in the upper reaches of the panhandle between March and April, it only takes place at the delta's southern tip in July and August. The Angolan-borne flood, therefore, reaches the distal end of the delta in the midst of the dry season, when the Kalahari Desert has been without rainfall for a significant period of time. This makes the Okavango Delta a true oasis within its semi-arid setting. The flood fills depressions, lagoons and floodplains and swells the banks of the Okavango Delta, producing a flood tide which contributes the other two thirds (Mendelsohn & El Obeid 2004) of the delta's water.

Only about 1.5% (Mendelsohn & El Obeid 2004) of the total volume of water entering the delta leaves via rivers such as the Thamalakane towards the Okavango's associated basins. Ninety six percent of the water is lost through evapotranspiration and a further 2.5% seeps into groundwater aquifers (Mendelsohn & El Obeid 2004; van As *et al.* 2012). When the flood is high enough, such as in 2010, 2011 and 2012, it reaches Lake Ngami by August and at that time travels down the length of the Boteti River to reach Lake Xau.

The flood tide that rhythmically fills the delta and then retreats, deposits its load of detritus which, together with decaying vegetation at the bottom of the lagoons and channels, forms a fibrous layer on which various aquatic plants are established. Eventually peat mats are formed, which are colonised by grass and result in widespread regions of peat bog. The grass clumps grow large enough to block the flow of water and eventually floodplain grasslands are formed (Ross 2003). The river channels which fill with sediment and dry, cause the waters to seek another course. This results in a constant switching of channels within the delta (Ross 2003; Mendelsohn & El Obeid 2004). Free-floating islands of papyrus may also form a plug and in a very short period of time cover a large lagoon. The wading of elephants may create new paths for water to pass through and the constant movement of hippos in and out of the water create trails which are eventually eroded by the flood waters to form new channels (Ross 2003). These changing channels play an important role in keeping the water of the delta fresh, in that it creates a variety of vegetation types and channels at different stages of development. Through this process, and by the activities of termites, islands are also formed on which large trees grow. Instead of the water merely evaporating, as in other wetlands in arid environments, water is mostly lost through evapotranspiration (Mendelsohn & El Obeid 2004). This is due to the rich concentration of vegetation in the delta. When water evaporates in areas such as the Makgadikgadi and Etosha Pans, salts become concentrated, but when drawn up the roots of plants, as in the Okavango, the salts carried by the water either remain in the plants or are concentrated in the soils beneath islands and permeate into the groundwater. The highest concentrations of salts in the delta are, therefore, in the centre of islands and the delta's water remains fresh (Ross 2003; Mendelsohn & El Obeid 2004). The Okavango Delta is, therefore, a unique biodiverse region in its semi-arid setting.

THE IMPORTANCE OF PULSE FLOODING IN SHAPING ZOOPLANKTON COMMUNITIES

The Okavango's pulse flooding also creates temporary floodplains. Such temporary floodplains in semi-arid regions are known to experience cycles of drying and flooding and the biotic responses to these are often referred to as 'boom' and 'bust'. Booms are pulses of phytoplankton and zooplankton productivity and are triggered by flooding and the accompanying pulse of nutrients delivered by flood waters and released from sediments (James *et al.* 2008). The 'bust' state refers to the dry period when water is limited. Dryland floodplains are characterised by variable productivity due to inconstant flood inundation in space and time (Thapa *et al.* 2015).

As previously mentioned, the 'boom' and 'bust' states of the Okavango's floodplains are driven by both local flooding during the wet (summer) season as well as flooding caused by another rain-borne event more than 1,000 km north of the delta. The flood from the Angolan highlands reaches the Okavango Delta in the midst of the dry season and as this water cascades down the river and channels it leaks into the peripheral floodplains, creating the second, but major, ‘boom’ state. Siziba *et al*. (2011a) stated that at times of low floods, floodplains may be inundated for four to six months, whereas during major flooding events, such as the 2010 flood, certain floodplains may maintain water for 12 months.

A number of studies (Høberg *et al.* 2002; Lindholm & Hessen 2007; Siziba *et al.* 2011a; 2011b; 2012) have pointed out that the Okavango’s temporary floodplains are important habitats for micro-crustaceans and are vital nursery sites for juvenile fish, as micro-invertebrates are the main prey for these juvenile fish and small fish species in the system.

Both ‘bottom up’ (resource supply) and ‘top-down’ (predation) forces are important in determining community structure and population dynamics amongst freshwater invertebrates. Rotifers are preyed on by organisms such as planktivorous fishes, macro-invertebrates and copepods and suffer competition from cladocerans, hence reducing their abundance (Wen *et al*. 2011). In the Okavango Delta, micro-invertebrates are an important food source during the critical stage of transition from newly hatched fish into late juvenile stages and are considered to be the main prey for both small fish species as well as juveniles of large fish species (Siziba *et al*. 2011a). Rotifers and other micro-organisms thrive in the temporary floodplains, making these environments important nurseries for juvenile fish. This indicates that the temporary floodplains are the main energy source of the system and the micro-invertebrates are extremely important in transferring energy from these floodplains to fish production (Siziba *et al*. 2011a).

Siziba *et al*. (2011a) found high densities of micro-invertebrates within the inundated grasses. They point out that this is a demonstration of the importance of inundated terrestrial grasslands in driving the aquatic food webs of the system. The terrestrial grasses of the Okavango Delta’s temporary floodplains are rich in wildlife dung and other organic material and shortly after flooding, nutrients are released from lakeside grasses, boosting aquatic productivity. The extent of flooding determines the size of micro-invertebrate populations as well as the subsequent juvenile fish production (Siziba *et al*. 2011a). The terrestrial environment which forms during the ‘bust’ or dry state plays a major role in the productivity of the temporarily flooded areas of the system.

Apart from the nutrients provided by the dung of wildlife and other organic material, terrestrial organisms, such as birds and elephants, also play an important role in maintaining the aquatic ecosystem. They are known to transport overwintering eggs and other propagules to rarely-flooded areas that have been dry for so long, that the original propagules deposited there may not be viable any more.

On the other hand, the ‘boom’ or aquatic state benefits the terrestrial or ‘bust’ state in that the sediment deposited by floodwater is advantageous for the growth of terrestrial plants once the flood resides. This, in turn, benefits the grazers and ultimately the predators of the Okavango grasslands. When floods recede, fish are trapped and become an important food source for terrestrial predators such as birds. Hence, the terrestrial and aquatic phases in these intermediate areas are completely dependent on one another and consequently, the permanent parts of the delta and farther off areas of the Kalahari Desert are indirectly also benefited by these temporary floodplains.

Traditionally, studies on aquatic biodiversity have mainly focussed on permanent water sources, but the significant contributions which temporary waters can make to species richness is increasingly being recognised. Previous studies have found that permanent water sources harbour a greater species richness than temporary water bodies, but that a substantial number of taxa would have been overlooked were the ephemeral habitats not examined (Walsh *et al.* 2014). This proved to be true during the present study of micro-invertebrates as well. Although most habitats sampled within the Okavango Delta and its associated basins are to some degree ephemeral, their period and frequency of inundation differs considerably in time. Habitats such as the Nxamasere Floodplain (Okavango Panhandle), the Ngarangi Floodplain (Okavango Panhandle) (see Fig. 4.1, **Chapter 4**) and the Thamalakane River (see Fig. 4.2, **Chapter 4**) are seasonally inundated to a lesser or greater extent, depending on flooding, but constantly have water on a yearly basis. Other habitats such as the Thaoge Channel (Okavango Delta Fan), Lake Ngami (see Fig. 4.2, **Chapter 4**), the Boteti River and Lake Xau (see Fig. 4.3, **Chapter 4**) experience decades of desiccation before receiving water and being refilled. Results show that the frequently inundated areas in the Okavango Panhandle and the Thamalakane River have a higher rotifer species diversity, but that the water bodies that are inundated once in decades produced species otherwise not present (e.g. *Asplanchnopus multiceps*, *Epiphanes senta* and *Synchaeta pectinata*).

From a conservation point of view, this study shows the importance of frequently inundated floodplains such as the Nxamasere floodplain (which had the highest species diversity) as well as the Okavango's infrequently inundated associated basins (which produced species otherwise not present) for the preservation of aquatic biodiversity. If, for example, water is extracted from the Kavango River in Namibia or damned back, as previously proposed by the Namibian Government, there will be a reduction in surface area and depth of floodplains and backwaters and a reduction in the total surface area of the Okavango Delta (Ashton 2000). The flood pulse, which is critical to the health and functioning of the system, will also be affected. Floodplains such as those at Nxamasere will cease to be inundated if the Okavango's natural cycle of flooding is affected. The floodplains, being shallow by nature, may be reduced to such an extent that they dry up completely. Ephemeral water bodies as in the case of Lake Ngami, the Boteti River and Lake Xau, which are reliant on unusually high flood cycles and outflow from the Okavango Delta, may remain dry permanently. This will have a devastating effect on not only the micro-invertebrate biodiversity of the region and consequently the fish, but on all fauna and flora of the system, including the terrestrial biodiversity and people.

FUTURE RESEARCH AND OTHER RECOMMENDATIONS

- If possible, when sampling zooplankton, live observations should be made and photomicrographs taken of live specimens. This is particularly important when studying the Rotifera. It was found that without the photomicrographs taken in the field, immediately after collection, a number of species would have been overlooked. Some species were no longer visible amongst preserved material, but could be identified from photomicrographs. Examples include the colonial rotifers, the Bdelloidea and families such as Synchaetidae. It is a well-known fact that *Synchaeta* is seldom identified up to species level in ecological and distribution studies, as fixatives distort general morphology of these soft-bodied organisms (Obertegger *et al*. 2006). Furthermore, live specimens maintain their natural colour and photomicrographs of these are of a better quality than that of preserved material.

- It was helpful to preserve samples in both 4% formaldehyde and 70% ethanol solutions as certain groups of organisms such as the rotifers preserved better in formaldehyde, while the Cladocera and Copepoda preserved best in ethanol.
- There is a lack of taxonomic research on southern African zooplankton species, without which comprehensive surveys of species richness and distribution is impossible. Amongst the Cladocera, for example, the Chydoridae require taxonomic revision, given that many species are most likely endemic and have not been described. Although the calanoid copepods have enjoyed taxonomic attention during the past two decades by researchers such as Dr. Nancy Rayner, vast areas of the subcontinent remain unexplored. Given that the calanoids have limited distribution ranges, it is very likely that unexplored areas may hold new, undescribed species. The possible new species of *Metadiaptomus* collected for the first time in the Okavango, following the high floods, serves as an example. We hypothesise that this species could have been washed down with the floods from wetland areas in the Okavango catchment.
- Taxonomic keys for identification are few and outdated. Rayner (1999) and Rayner (2001) are extremely helpful for the identification of the southern African Calanoida and that of Seaman *et al.* (1999) and Kořínek (1999) are useful for certain Cladocera species. These, however, exclude the Chydoridae, which is unsurprising given that this group is in need of taxonomic revision. There is a lack of proper keys to follow for the identification of the southern African freshwater Cyclopoida, the last major taxonomic work on cyclopoids in southern Africa being that of Sars (1927) and Kiefer (1929).

- In the study area of the Okavango Delta and its associated basins specifically, it is recommended that future research be conducted on the taxonomy of individual taxa, specifically that of the Chydoridae, Cyclopidae and Ostracoda.
- Future research should also focus on the zooplankton egg banks of the seasonally flooded floodplains as this may produce more species to the list of zooplankton in the Okavango Delta and its associated basins.
- In the Nata River, much research remains to be conducted since the present study was the first to explore the zooplankton of this important resource and only took place during the dry season, at low water levels. It is, therefore, likely not a complete census of the zooplankton of the system.
- The Nata River which almost definitely dries up seasonally and during some years does not receive water at all, provides the perfect opportunity to try to identify possible dormant stages of the epibiont, *Trichodina diaptomi,* found associated with the calanoid copepod, *Metadiaptomus transvaalensis*. The host most definitely enters a dormant stage during times of drought and *Trichodina diaptomi* has not been discovered on any other intermediate host.

CONCLUDING REMARKS

The present study has pointed out large gaps in zooplankton research, in not only Botswana, but southern Africa as a whole. This work has laid down the foundation in our knowledge on the subject, but due to its scope, it has not allowed for in-depth taxonomic research. Such taxonomic research into specific groups of organisms is vital for future biodiversity surveys. As a result of challenges the subcontinent has faced, such as war and the recent political isolation of South Africa, freshwater research has been neglected. Countless research opportunities exist and given that the zooplankton form such vital links in the food webs of aquatic ecosystems, it is important that funding be made available for zooplankton research. The vast majority of people in southern Africa live below the poverty line and in the Okavango Delta, most survive only because of the natural resources that the rivers and swamps provide.

Unfortunately, the Okavango Delta and its associated basins face many threats, not only from the growing local human population, but also from activities upstream. The

Okavango River is shared by three basin states, namely Angola, Namibia and Botswana. In Angola, the river has mostly remained untouched, due to the ravages of war making it inaccessible. Lately, however, the country has strong oil revenues and the human population is growing at a rapid rate. This, together with an increase in agricultural activities, is placing greater pressure on the tributary rivers in the Angolan highlands. Recently, a rice farming program was devised, together with China, wherein rice plantations are being planted in the river floodplains. This may have negative effects on the biodiversity of the region, but also on that of the downstream Okavango Delta.

Namibia is an extremely arid country and the majority of its water sources are situated in the far north. The Okavango River is one of the country’s major water sources and the Namibian Government has devised a number of plans to utilise its water. These include using the river for agriculture and power generation as well as to transfer water to supply the country’s capital, Windhoek. The damming back of the Okavango River or the extraction of large volumes of water will have devastating effects on the Okavango Delta in the semi-arid Botswana.

The proper functioning of the Okavango Delta is entirely reliant on the pulse flooding of the Okavango River. Without the annual flooding, the delta’s waters may cease to remain fresh, due to its setting in a semi-arid environment, where evaporation rates surpass precipitation three-fold. This will have devastating effects on the biodiversity of the region. Furthermore, if the volumes of water reaching the delta are decreased, the delta’s surface area will shrink to a great extent, given its shallow nature. The temporarily flooded floodplains, which are vital for energy transfer between the terrestrial and aquatic ecosystems, will no longer receive water. This, in turn, will affect phytoplankton and zooplankton production and consequently the production of fish and other organisms higher up in the food web. Large numbers of elephants, ungulates and other animals in the Kalahari Desert migrate to the delta during the dry season, as the Okavango’s floods arrive in the delta at a time when the Kalahari has been without any surface water for months. Not only will the aquatic biodiversity of the Okavango Delta be affected, but that of the surrounding Kalahari Desert as well. Furthermore, the majority of the human population in the region of the delta live below the poverty level and are completely reliant on the water and other resources the Okavango Delta provides for their livelihoods.

Fortunately, the Permanent Okavango River Basin Commission (OKACOM) was formed by all three the basin states (Angola, Namibia and Botswana) to promote the sustainable management of the Okavango River Basin. Data on the functioning and biodiversity of the system is important for assisting with decision-making processes and research should thus be a focal point in the conservation of the Okavango Delta, the 'jewel of the Kalahari' and one of Africa's last remaining wetland wildernesses.

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Abstract & Uittreksel

ABSTRACT

The Okavango Delta, one of the most iconic wetlands on the planet, is the third largest Ramsar site and in 2014 was listed as the 1000th UNESCO World Heritage Site. It is situated in the centre of the Kalahari Basin of southern Africa, which is a semi-desert and the largest continuous sea of sand on earth. The Okavango Delta, in northern Botswana, receives its waters from the Okavango River which originates as many tributaries in Angola and flows as a single river through Namibia's Caprivi Strip before entering Botswana where it is met by a series of fault lines. These faults control the shape of the delta and result in its water spreading across the Kalahari Sands, forming the world's largest alluvial fan. Most years there is little to no outflow from the Okavango Delta, but the system recently experienced consecutive years of record high floods from the catchment area in Angola, resulting in the basins associated with the delta being inundated for the first time in up to four decades. This provided the perfect opportunity to study the zooplankton of the Okavango Delta, from which only a few studies have been conducted, and it has allowed an insight into the zooplankton species diversity of the associated basins. The aims of the present study were to obtain specimens of aquatic micro-invertebrates, correctly identify Rotifera and micro-Crustacea material collected up to species level where possible, create a photographic data base of the organisms and to map the distribution of each species throughout the study area. Water bodies included in the study are the Okavango Panhandle, the Okavango Delta Fan, the Thamalakane River, Lake Ngami, the Boteti River and Lake Xau. A total of 33 rotifer species were identified, including three genera (*Asplanchnopus* de Guerne, 1888, *Synchaeta* Ehrenberg, 1832 and *Sinantherina* Bory de St. Vincent, 1826) and six species, i.e. *Asplanchnopus multiceps* (Schrank, 1793), *Epiphanes senta* (Müller, 1773), *Synchaeta pectinata* Ehrenberg, 1832, *Conochilus dossuarius* Hudson, 1875, *Conochilus unicornis* Rousselet, 1892 and *Sinantherina* sp., which have not been identified from the waterways of northern Botswana before. The cladoceran species diversity, excluding the family Chydoridae which was the most diverse, but lacks taxonomic review, totalled 12 species. Amongst these was the species *Macrothrix propinqua* Sars, 1909 which has not been recorded from the study area previously. The calanoid copepod *Tropodiaptomus schmeili* (Kiefer, 1926) was present in the

Okavango Delta and its associated basins, except in Lake Xau where no calanoids were collected. Furthermore, a possibly undescribed species of *Metadiaptomus* Methuen, 1910 was found in the Okavango Panhandle and Lake Ngami. Eight species of the order Cyclopoida were collected from the Okavango Delta and its associated basins, five of which were recorded from the system for the first time. Zooplankton studies were also conducted in the Nata River during low flow and results indicated a total of 14 rotifer, cladoceran and copepod species. Unlike the Okavango System where the calanoid genus *Tropodiaptomus* thrives, *Metadiaptomus transvaalensis* Methuen, 1910 was found in the Nata River. Furthermore, this calanoid copepod was infested with the peritrich, *Trichodina diaptomi* Šrámek-Hušek, 1953, of the order Mobilida. Notes on the possible life-history of this trichodinid are provided. The results from the entire study have laid down the framework for future zooplankton research in the waterways of the semi-arid Botswana, where no baseline data exists for many of the life-sustaining water bodies.

Keywords: Boteti River, Cladocera, Copepoda, distribution, Lake Ngami, Lake Xau, Nata River, Okavango, Rotifera, species diversity, Thamalakane River

UITTREKSEL

Die Okavangodelta, een van die ikoniese vleilande op die planeet, is die derde grootste Ramsargebied en is sedert 2014 as die 1000ste UNESCO Wêrelderfenisgebied gelys. Dit is in die sentraal Kalahari-kom, in suider-Afrika, geleë, wat ‘n halfwoestyn-area is en ook die grootste sandmassa op aarde is. Die Okavangodelta, in noordelike Botswana, word deur die Okavangorivier gevoed, met die oorsprong uit ‘n aantal bergstrome en sytakke vanuit Angola. Die rivier vloei deur die Kaprivistrook van Namibië, na Botswana waar die water oor die Kalaharisand uitsprei en ‘n delta vorm, as gevolg van ‘n reeks geologiese verskuiwings in die aardkors. Hierdie verskuiwings beheer die vorm van die delta, bepaal die verspreiding van die water oor die Kalaharisand en vorm die wêreld se grootste alluviale delta. Meeste jare was daar geen of baie min uitvloei vanuit die Okavangodelta, maar hierdie stelsel het vir die laaste paar agtereenvolgende jare rekord vloede vanaf die opvangsgebied in Angola ontvang. Dit het veroorsaak dat die efemere riviere en mere wat met die delta geassosieer word, vir die eerste keer in jare opgevul het. Hierdie verskynsel het ‘n gulde geleentheid gebied om die soöplankton-spesiediversiteit van die Okavangodelta en die geassosieerde waterliggame te bestudeer, aangesien daar min inligting hieroor bekend is. Die doel van die studie was om akwatiese mikro-ongewerwelde spesies te versamel, die Rotifera en mikro-Crustacea tot en met spesievlak te identifiseer, waar moontlik, en om ‘n fotografiese databasis asook verspreidingskaarte van die organismes saam te stel. Die waterweë wat deel van die studie gevorm het, sluit die Okavangopypsteel, die Okavangodelta, die Thamalakanerivier, Ngamimeer, die Botetirivier en Xaumeer in. In totaal is 33 Rotifera-spesies geïdentifiseer, waarvan drie genera (*Asplanchnopus* de Guerne, 1888, *Synchaeta* Ehrenberg, 1832 en *Sinantherina* Bory de St. Vincent, 1826) en ses spesies, nl. *Asplanchnopus multiceps* (Schrank, 1793), *Epiphanes senta* (Müller, 1773), *Synchaeta pectinata* Ehrenberg, 1832, *Conochilus dossuarius* Hudson, 1875, *Conochilus unicornis* Rousselet, 1892 en *Sinantherina* sp. vir die eerste keer in die studiegebied versamel is. Die Cladocera-spesiediversiteit, uitsluitend verteenwoordigers van die familie Chydoridae, het uit 12 spesies bestaan. Laasgenoemde sluit die spesie *Macrothrix propinqua* Sars, 1909 in, wat ook tydens die opnames vir die eerste keer versamel is. Die Calanoida-spesie *Tropodiaptomus* *schmeili* (Kiefer, 1926), was in die Okavangodelta en al die verwante waterliggame teenwoordig, uitsluitend Xaumeer. ‘n Moontlike nuwe spesie van die genus *Metadiaptomus* Methuen, 1910 is in beide die Okavangopypsteel en Ngamimeer versamel. Agt spesies van die orde Cyclopoida was in die Okavangodelta en verwante waterliggame versamel, waarvan vyf vir die eerste keer in hierdie stelsel aangeteken is. Soöplankton studies is ook in die Natarivier, tydens ‘n periode van verlaagde watervlakke, uitgevoer. Die resultate van laasgenoemde studie sluit 14 soöplanktonspesies (verteenwoordigers van Rotifera, Cladocera en Copepoda) in. In teenstelling met die Okavangostelsel, waar verteenwoordigers van Calanoida meestal deur die genus *Tropodiaptomus* verteenwoordig was, was slegs *Metadiaptomus traanvaalensis* Methuen, 1910 in die Natarivier versamel. Hierdie spesie was met ‘n verteenwoordiger van die Peritrichia, *Trichodina diaptomi* Šrámek-Hušek, 1953, orde Mobilida, besmet. Inligting rakende die potensiële lewensstrategie van hierdie spesie word ook verskaf. Die resultate van die hele studie vorm die basis vir toekomstige soöplanktonstudies in die waterweë van die semi-ariede Botswana, waarvoor daar tot op hede vir ‘n groot aantal van hierdie lewensonderhoudende waterliggame, geen grondslagdata en inligting beskikbaar was nie.

Sleutelwoorde: Botetirivier, Cladocera, Copepoda, Ngamimeer, Natarivier, Okavango, Rotifera, spesiediversiteit, Thamalakanerivier, verspreiding, Xaumeer

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Appendix

APPENDIX

Appendix 1: Arithmatic mean averages of physical water quality parameters measured in the Okavango Delta and its associated basins in August 2011, August & September 2012 and July 2013.

STUDY SITE	Water temperature (°C)	pH	Dissolved Oxygen (%)	Dissolved Oxygen (ppm)	Conductivity (µS/cm)	Total Dissolved Solids (ppm)	Salinity (PSU)
Okavango Delta Panhandle							
Mohembo Pool	21.42	8.61	86.1	6.65	195	98	0.09
Ngarangi Floodplain	18.32	7.25	18.8	1.57	45	22	0.02
NX01	16.6	7.92	50.5	4.34	172	105	0.09
NX02	21.03	7.41	85.2	6.65	214	107	0.1
NX03	20.54	8.01	64.1	5.05	268	135	0.13
NX04	26.15	8.43	105.9	7.5	402	201	0.19
NX05	21.31	8.56	83.2	6.66	199	139	0.09
NX06	20.03	8.09	47.6	3.84	352	176	0.17
NX07	16.93	8.32	53.5	4.61	287	143	0.14
NX08	NA	NA	NA	NA	NA	NA	NA
NX09	20.78	9.07	98.2	7.92	189	132	0.09
NX10	NA	NA	NA	NA	NA	NA	NA
NX11	21.96	7.86	37.2	2.9	398	199	0.19
NX12	20.6	8.76	80.8	6.4	303	209	0.14
NX13	18.97	8.39	74.4	6.34	335	236	0.16
NX14	19.74	8.96	93.4	7.72	201	140	0.09
NX15	17.43	8.23	65.1	5.78	284	199	0.14
Ikoga	NA	NA	NA	NA	NA	NA	NA
Average	**20.12**	**8.26**	**69.6**	**5.60**	**256**	**149**	**0.12**
Okavango Delta Fan							
Thaoge Tsau	22.01	7.1	77.8	5.99	88	44	0.04
Maun03	21.43	7.22	76.4	5.96	97	49	0.04
Maun05	18.22	8.72	88.3	7.34	173	87	0.08
Average	**20.55**	**7.68**	**80.8**	**6.43**	**119**	**60**	**0.05**

Appendix 1 (Cont.): Arithmatic mean averages of physical water quality parameters measured in the Okavango Delta and its associated basins in August 2011, August & September 2012 and July 2013.

STUDY SITE	Water temperature (°C)	pH	Dissolved Oxygen (%)	Dissolved Oxygen (ppm)	Conductivity (µS/cm)	Total Dissolved Solids (ppm)	Salinity (PSU)
Thamalakane River							
Maun01	19.01	7.28	61.2	5.1	153	107	0.07
Maun02	22.28	7.64	74.6	5.85	165	109	0.07
Maun04	23.15	7.33	67	5.06	145	73	0.07
MaunTJL	23.91	6.47	78.6	5.83	97	48	0.04
Average	**22.09**	**7.18**	**70.4**	**5.46**	**140**	**84**	**0.06**
Lake Ngami							
Nhabe	21.54	7.86	72.6	5.77	112	78	0.05
LN01	20.17	7.43	89.5	7.21	166	97	0.08
LN02	18.73	7.64	97.1	8.1	181	90	0.09
LN03	19.51	7.98	97.7	8.04	163	81	0.08
Average	**19.99**	**7.73**	**89.2**	**7.28**	**156**	**87**	**0.08**
Boteti River*							
Makalamabedi01 (2011)	15.97	7.43	52.2	4.6	194	136	0.09
Makalamabedi02 (2012)	19.11	7.53	2.4	0.19	103	51	0.05
Motopi (2011)	18.92	7.55	76.1	6.35	112	78	0.05
Motopi (2012)	6.79	7.14	3	0.27	104	52	0.05
Xhumo Bridge (2011)	21.65	7.39	69.2	5.5	131	92	0.06
Xhumo Bridge (2012)	20.46	7.4	3	0.24	143	76	0.07
Average	**17.15**	**7.41**	**34.3**	**2.86**	**131**	**81**	**0.06**

*Physical water quality results obtained in both 2011 and 2012 are provided for sites in the Boteti River to indicate the significant difference in oxygen concentration between the two consecutive years.

Appendix 1 (Cont.): Arithmatic mean averages of physical water quality parameters measured in the Okavango Delta and its associated basins in August 2011, August & September 2012 and July 2013.

STUDY SITE	Water temperature (°C)	pH	Dissolved Oxygen (%)	Dissolved Oxygen (ppm)	Conductivity (µS/cm)	Total Dissolved Solids (ppm)	Salinity (PSU)
Lake Xau							
LX01	18.01	7.46	57.4	4.89	262	183	0.12
LX02	22.26	7.43	76.6	5.94	188	131	0.09
LX03	21.33	8.51	89	7.09	160	112	0.07
LX04	16.01	9.04	183.5	16.05	1604	802	0.82
LX05	16.89	8.6	171.7	14.26	205	102	0.1
Average	**18.9**	**8.21**	**115.6**	**9.65**	**484**	**266**	**0.24**