An annotated checklist of the freshwater bivalves (Mollusca: Bivalvia) of Botswana and Namibia

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An annotated checklist, including 18 species of freshwater bivalve belonging to five families, recorded from Botswana and Namibia, is provided. New morphometric information is provided for the species *Mutela zambesiensis* Mandahl-Barth and *Spathopsis petersi* (von Martens), and features of shell morphology are illustrated for *Pisidium reticulatum* Kuiper using stereoscan microscopy. The majority of species occur in the well-watered northerly regions of these countries. Fifty percent of these are widely distributed tropical African species at, or close to, the southerly limits of their ranges, seven species (39%) are categorised as general 'southern African', and two species (11%) appear to be confined to the south-central African region. Although no endemic bivalve species are recorded from the study area, further research may show that the large *Chambardia* from the Kunene River is *C. moutai* (Dartevelle) and not *C. wahlbergi* (Krauss) as reported here and that *C. moutai* may be restricted to the Kunene River. Four species are new to Botswana, namely: *Chambardia petersi* (von Martens), *Coelatura mossambicensis* (von Martens), *Pisidium reticulatum* Kuiper and *P. viridarium* Kuiper; and one species to Namibia, namely: *Eupera parasitica* (Deshayes).

Keywords: Mollusca, bivalves, ecology, checklist, Africa, Namibia, Botswana.

INTRODUCTION

Connolly's (1931) report on the non-marine molluscs of Namibia (as South West Africa), and subsequent (1939) monograph dealing with the non-marine molluscs of southern Africa as a whole, have remained the most comprehensive accounts of the freshwater bivalve fauna of Namibia and Botswana (formerly Bechuanaland). This is surprising, in view of the fact that bivalves (Bivalvia) constitute the major component of the benthos of many freshwater habitats, for example, in Lake Kariba, Zimbabwe, where these accounted for 96% of the infaunal biomass (Machena & Kautsky 1988). Much additional material has been collected during the 65 years since Connolly's work. The Unionoida of the northern parts of Botswana and Namibia were included in a review of the superfamily in south-central Africa by Appleton (1979). Further records of these and other families have been given by Appleton *et al.* (2003), Curtis & Appleton (1987), Curtis (1991, 1997, 1999), Daget (1998), de Moor *et al.* (2000), Kuiper (1964, 1966a, 1966b), Mandahl-Barth (1988), and van Bruggen (1980). This checklist updates knowledge of the

freshwater Bivalvia of Botswana and Namibia from these sources and from material collected by staff of the then State Museum of South West Africa (now National Museum of Namibia), the South West African Department of Water Affairs (now Directorate of Water Affairs), the Albany Museum and the AquaRAP 2000 Expedition to the Okavango Delta (Appleton *et al.* 2003).

Namibia is an arid to semi-arid country extending over 11½ degrees of latitude (17–28½°S) and, except for the Caprivi Strip, 9 degrees of longitude (11–21°E) (Figure 1). The narrow Caprivi Strip extends 4½ degrees further eastwards to the upper Zambezi River. The freshwaters of Namibia are dominated by four perennial river systems: the Gariep (Orange) River in the south, the Kunene River in the north-west, Okavango and Zambezi Rivers in the north-east, and the Kwando-Linyanti system in the Caprivi. The first mentioned rises in the mountains of Lesotho and the last three mentioned all rise in southern Angola. De Moor *et al.* (2000) provide a useful description of the Kunene River from the Ruacana Falls to the Southern Atlantic.

Botswana (Figure 1) is also arid and covers 9 degrees of latitude (18–27°S) and 9 degrees of longitude (20–29°S). The major source of water is the wetland system in the north-west quadrant of the country, that incorporates the Okavango Delta and the swamps associated with the Linyanti River in the central-north. The catchments of the Kunene, Okavango and Zambezi Rivers drain much of south-central Africa and abut that of the Zaïre River.

The proximity of the rivers in the northern parts of the study area to the Zaïre system (Figure 1), a major centre of mollusc endemism (Brown 1994; Dudley 2001; Pilsbry & Bequaert 1927), is reflected in the high proportion of tropical forms in the bivalve fauna of these systems (i.e. Kunene, Okavango and upper Zambezi Rivers and the wetlands of the Eastern Caprivi) and which is distinct from those in the eastern (Limpopo) and southern (Gariep) systems. In addition to the Okavango Delta in Botswana, there are two other endorreic basins, the ephemeral Cuvelai/Ekuma/Etosha system in central northern Namibia and the perennial Kwando/Liambezi/Linyanti system in eastern Caprivi. The eastern half of northern Botswana is drained by the eastwards-flowing Limpopo River system. The vast interiors of both countries are drained by numerous seasonal watercourses with many isolated artesian and other springs in the north-central region.

MATERIAL AND METHODS

An annotated checklist to the bivalves of Botswana and Namibia is provided that includes 18 bivalve species in 10 genera and five families. With a few exceptions, genera and species are arranged following Mandahl-Barth (1988); the most comprehensive account of the freshwater bivalves of Africa. It should be noted, however, that the

Figure **1**. Map of central and southern Africa, indicating the study area of Botswana and Namibia.

above-mentioned work makes several important changes to the synonomy of the genera *Corbicula* von Mühlfeld, *Eupera* Bourguignat and *Mutela* Scopoli. Locality records cited by Appleton (1979) are not repeated here, except where considered necessary; details of all additional specimens examined during the course of the study are cited below. Illustrations of all species cited here, except *Pisidium reticulatum* Kuiper are provided by Appleton (1996, 2002).

The SEM micrographs of *P. reticulatum* (Figures 6–8), were taken by use of a Philips XL 30 stereoscan microscope at the Centre for Electron Microscopy, Pietermaritzburg Campus, University of KwaZulu-Natal, South Africa.

Abbreviations used in the text: AMGS = Albany Museum, Grahamstown, South Africa; NMNW = National Museum of Namibia, Windhoek, Namibia (formerly the State Museum of South West Africa (SMN)); NMSA = Natal Museum, Pietermaritzburg, South Africa; UKZN = University of KwaZulu-Natal, Durban, South Africa. The prefixes 'KUN' and 'SMN' refer to the accession numbers of specimens housed in the Albany Museum and the National Museum of Namibia, respectively. * = new country record.

SYSTEMATICS

CLASS: BIVALVIA
SUPERFAMILY: UNIONOIDA

FAMILY: UNIONIDAE

Genus: *Unio* Philipsson, 1788
TYPE SPECIES: *Mya pictorum*

Unio caffer Krauss, 1848
DISTRIBUTION: Malawi, Mozambique, Namibia, South Africa, Zambia and Zimbabwe.
MATERIAL: **Namibia**: Gariep (formerly the Orange) River, 1 specimen, between Sandfontein and Grasdrif [SE2817Ad], 1981, J. Coetzee (SMN76090) (NMNW); 4 empty specimens, Lorelei on north bank east of Sendelingsdrif, 28°05'S, 16°53'E, 26.xi.1980, R. van der Westhuizen (UKZN); 7 empty specimens, Vioolsdrift [SE2817Dc], 16.vii.1980, R. Jubb (UKZN).
PUBLISHED RECORDS: Vioolsdrift and Daberas Deposit (28°18'S, 16°49'E) (Palmer 1996).
NOTES: *Unio caffer* is endemic to southern Africa, from approximately 14°S in Malawi, to the Western Cape, South Africa, where it has become rare, or possibly extinct, in some rivers and *vleis* (J.A. Day pers. comm.). New data support Connolly's (1931, 1939) record from Stolzenfels on the Gariep (Orange) River. In Namibia, therefore, it is found only in the extreme south, in the lower reaches of the Gariep River and its tributaries. The only record from Botswana is as a sub-fossil associated with the southward-flowing Nosob-Hygap River, a tributary of the Gariep River (Connolly 1939). The wide geographical separation of *U. caffer* from the only other species of *Unio* occurring in Africa, i.e. *U. abyssinicus* Martens, 1886, and *U. elongatulus* C. Pfeiffer, 1825, from Ethiopia and north-west Africa (van Damme 1984), led Mandahl-Barth (1988) and Graf & Cummings (2006) to follow Connolly (1925), Modell (1964) in placing it in the genus *Cafferia* Simpson, 1900. They do not refer to a review of the branchial anatomy and systematic position of this species by Heard & Vail (1976), which concluded that it should be retained in *Unio*. This latter opinion is followed here.

Genus: *Coelatura* L. Pfeiffer, 1877
TYPE SPECIES: *Unio aegyptica*
NOTES: The writers follow Rosenberg *et al.* (1990), who pointed out that the commonly used spelling of the name for this large genus, *Caelatura* Conrad, 1853, is incorrect, and that the later name, *Coelatura* L. Pfeiffer, 1877, should rather be used. This genus is widely distributed in Africa, but only two of the many described species are recorded from the study area.

Coelatura kunenensis (Mousson, 1887) (*Unio*)
DISTRIBUTION: Angola, Botswana, Namibia and Zambia.
PUBLISHED RECORDS: **Botswana**: Okavango Delta, sandbanks on the Okavango River, near Shakawe [SE18 21Bd], 8.vi.2000; Moremi Game Reserve, in mud in Gadikwe Lagoon [SE1923Aa] 14.vi.2000 (Appleton *et al.* 2003).
MATERIAL: **Botswana**: Okavango Delta, 4 specimens, Boro River, 19°25'97"S, 22°56'08"E, 13.xii.1996, B.A. Curtis (SMN77019); 2 specimens, same except: 19°27'81"S, 22°57'07"E, 14.xii.1996 (SMN77027); 2 specimens, same except: 19°26'88"S, 22°56'23"E (SMN77031) (all

NMNW); 72 specimens, Chief's Island, Nxaraga Lagoon [SE1923Ca], 10.iii.1984, C.C. Appleton (UKZN); 97 specimens, Thamalakane River at Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN); **Namibia**: Kunene River, 1 pair valves, on banks of floodplain at Palm Grove campsite, Oonjana, 17°00'18"S, 13°25'52"E (site 9 of de Moor *et al.* 2000), 17.xi.1997, F.C. de Moor & S. Bethune (KUN62A) (AMGS). Okavango River, 2 specimens, at: 17°52'67"S, 20°17'64"E, shallow sand, 31.x.1996, B.A. Curtis (SMN76953); 2 specimens, at: 18°00'50"S, 20°44'95"E, shallow with sand, 1.xi.1996, B.A. Curtis (SMN77016); 2 specimens, at: [SE1821Bd], sandbank, 10.xii.1996, B.A. Curtis (SMN76995); 1 juvenile, 45.4 km upstream of Rundu, Mabunya [SE1719Ca], 29.x.1996, B.A. Curtis (SMN76942); 3 specimens, 24.2 km west of Rundu [SE1719Cb], 29.x.1996; B.A. Curtis (SMN76930); 1 juvenile, Rundu slipway [SE1719Dc], 10.vii.1986, P. Skelton & G. Merron (SMN76271): 1 specimen, Ndonga, Omataka confluence [SE 1720Cd], 6.iii.1984, S. Bethune (SMN76122); 16 specimens (including 5 juveniles), Nyangana Omarumba, Okavango floodplain [SE 1820Ba], 12.vi.1983, S. Bethune (SMN76821/SMN76828); 1 specimen, Manuingombe [coordinates unknown], 11.vi.1983, S. Bethune (SMN76822); 17 specimens + 3 left & 1 right valves, Andara Mission [SE1821Ab], 8.iii.1984, C.C. Appleton (SMN76046); 1 specimen, Andara [SE1821Ab], 24.viii.1971, M.J. Penrith (SMN75399); 2 specimens, Popa Falls [SE1821Ba], 21.x.1984, S. Bethune (SMN76109a); 2 specimens, same except: 30.viii.1971, M.J. Penrith (SMN75374); 1 specimen, sandbank below Popa rapids [SE1821Ba], x.1984, P. Skelton & G. Merron (SMN76270) (all NMNW). Eastern Caprivi: 3 specimens, mulapo at Sanzo [SE1721Dc], [undated], A.C. Evans (SMN76823); 1 specimen + 1 left valve, Lizauli [SE1823Ab], 15.vi.1982, T.F. Jackson (SMN76824); 1 specimen, Zambezi floodplain, pool opposite Hippo Island [SE1724Ad], 14.vi.1983, S. Bethune (SMN76825); 1 specimen same except: (SMN76826); 1 juvenile, Zambezi floodplain, off Hippo Island [SE1724Ad], 9.xii.1982, S. Bethune (SMN75948); 6 specimens, including 2 juveniles, Sesheke on Zambezi River [SE1724Ad], [undated], C.J. Schutte (SMN76827); 3 specimens, Lake Lisikeli [SE1724Cb], 14.xii.1982, S. Bethune (SMN76088); 2 juveniles, Kwando River [locality unknown], [undated], C.D. Dettman (SMN76829); 2 specimens, Kwando floodplain, Sitwe [SE1723Cd], 15.xii.1982, S. Bethune (SMN75928); 1 specimen, Zambezi floodplain, Maninge Manzi [SE1724Ad], 10.vi.1983, S. Bethune (SMN76830) (all NMNW).

NOTES: This species was described from the Kunene River, but Mandahl-Barth (1988) followed Connolly (1931, 1939), in uniting it with material from the Okavango and upper Zambezi systems. It appears to be confined to these river systems and is, without doubt, the most common bivalve species in the study area. Both the above and earlier records (Appleton 1979; Appleton *et al.* 2003; Connolly 1931, 1939; Curtis 1997; Curtis & Appleton 1987; van Bruggen 1980) indicate that it occurs at numerous localities on the Kunene, Okavango and upper Zambezi, where these form the northern borders of Namibia and Botswana. These are formed by the Kwando/Linyanti system in eastern Caprivi, the Ekuma floodplain, part of the endorrheic Etosha system in Namibia, and the Okavango Delta in Botswana. The species is also common in Iron Age midden sites at Itezhitezhi, in the Kafue Valley, Zambia (Appleton 1985).

TAXONOMIC NOTES: As noted by Appleton (1979) and Mandahl-Barth (1988), the shell shape of *C. kunenensis* is variable. Those from the Kunene, Kafue and upper Zambezi Rivers are, in general, shorter and darker than those from the Okavango River and Delta, and thus vary significantly in terms of L/H *vs.* L ($p<0.001$) (Appleton 1979). The L/Hmax ratio is higher relative to shell length in the Kunene specimens, particularly in larger examples, than in those from the Okavango River. Nevertheless, Mandahl-Barth (1988) regarded these as the same species, even

though he had not seen material from the Kunene. Young shells, to a length of approximately 20 mm, typically have a chevron sculpture and greenish rays over the shell. As noted above, in terms of morphometrics, however, the populations in the Okavango system appear different from those in the Kunene, Kafue and upper Zambezi systems (Appleton 1979). This requires to be investigated further, as does the relationship between this species and *C. choziensis* (Preston, 1910), from the Luapula River and Lake Bangweulu in northern Zambia (Mandahl-Barth 1968).

Coelatura mossambicensis (von Martens, 1860) (*Unio*)

DISTRIBUTION: Botswana*, Malawi, Mozambique, Tanzania and Zimbabwe.

MATERIAL: **Botswana**: Limpopo River, 1 specimen, Stevensford Game Reserve [2227Db/Dd/2228Ca/Cc], 13.iii.1984, B. van der Waal (UKZN).

NOTES: A south-east African species restricted to the lower Zambezi (including Lake Kariba) in Malawi, Mozambique and Zimbabwe (Appleton 1979; Mandahl-Barth 1988). In the present study area, it is reported only from the Limpopo River in the north-east corner of Botswana. Kenmuir (1980a, 1980b, 1980c), provide information on the ecology, growth and reproductive biology of *C. mossambicensis* in Lake Kariba and Appleton & la Hausse de Lalouviere (1987) on the density of *C. framesi* Connolly, 1925, on the Pongolo River floodplain, South Africa.

TAXONOMIC NOTES: Mandahl-Barth (1988) proposed that *C. mossambicensis* be synonymised with the larger *C. framesi* which occurs further south in Mozambique, South Africa and Zimbabwe, but until such time as the two species are better known, it seems advisable to treat these as separate species.

FAMILY: IRIDINIDAE

Genus: *Aspatharia* Bourguignat, 1885

TYPE SPECIES: *Margaritana vignonana*

Aspatharia (*Aspatharia*) *pfeifferiana* (Bernardi, 1860) (*Margaritana*)

DISTRIBUTION: Widely distributed across central and southern Africa, including: Angola, Botswana, Democratic Republic of Congo, Namibia and Zambia.

MATERIAL: **Botswana**: Okavango Delta, 2 specimens, Thamalakane River, near Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN). **Namibia**: Kunene River, 1 pair valves, on bank of floodplain at Palm Grove campsite, Oonjana, 17°00'18"S, 13°25'52"E (site 9 of de Moor *et al.* 2000), 17.ix.1997, F.C. de Moor (KUN62B) (AMGS). Okavango River, 2 specimens, ±39 km E of Rundu, shallow and sandy, 17°54'61"S, 20°06'43"E, 31.x.1996, B.A. Curtis (SMN76948); 5 specimens, Andara Mission [SE1821Ab], 8.iii.1984, C.C. Appleton (SMN76050) (all NMNW).

NOTES: A distinctive species, widely distributed across southern and central Africa, from Chad to Zimbabwe. In the study area, the above localities, plus those provided by Appleton (1979), Connolly (1931, 1939) and Curtis (1997), indicate that the species occurs in the Kunene, upper Zambezi and Okavango Rivers in Namibia and the Okavango Delta in Botswana. These systems represent the southern range limit of the species in Africa. It is nowhere common and juveniles have not been found. Graf & Cummings (2006) suggest that these may be referable to *A. subreniformis* (Sowerby, 1867) described from Malawi but that more material is needed.

Genus: *Chambardia* Servain, 1890

TYPE SPECIES: *Chambardia letourneuxi*

NOTES: The use of the generic name *Chambardia* is contentious and requires justification. Daget (1998) revived the name *Chambardia* Servain (1890) for the following two species despite its earlier rejection by van Damme (1984), Mandahl-Barth (1988) and Appleton (1996) in favour of *Spathopsis* Simpson, 1900. Daget (1998) argued that because the types of both genera were generally considered subspecies of *S. wahlbergi* (Krauss, 1848), they were synonymous and that the older synonym, *Chambardia*, should have priority. Mandahl-Barth (1988) did not mention *Chambardia* at all, recognising the genus *Spathopsis* and two species-groups within it, the Wahlbergi- and Rubens-groups. These are included below under the name *Chambardia*, but only the former group is found in southern Africa and the two species allocated to it both occur in the study area. Appleton (2002) followed Daget's 1998 use of the name *Chambardia* instead of *Spathopisis* and the writers also do so here.

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

DISTRIBUTION: Widely distributed across Africa, including: Angola, Botswana, Chad, Egypt, Kenya, Malawi, Mozambique, Namibia, Senegal, South Africa, Tanzania and Zimbabwe.

NOTES: This is the largest freshwater bivalve in Africa. This widely distributed species was, as reported by Appleton (1979), formerly known as *Aspatharia* (*Spathopsis*) *wahlbergi* or *Spathopsis wahlbergi*, and is apparently uncommon in the study area. It was collected from the Kunene River at Ruacana (SMN75597, 17°24'05"S, 14°12'55"E) and from the upper Kunene River in southern Angola by Dartevelle (1939). There is a single record from the Kavango River at its junction with the Omataka-Omarumba (Ndonga, 17°57'S, 20°59'E) (Connolly 1939), but it has not been reported again from this river and has never been collected in the Okavango Delta. Appleton (1979) recorded it from the Nata River in north-eastern Botswana; the westernmost tributary of the eastwards-flowing Limpopo system. Both Mandahl-Barth (1988) and Daget (1998) recognised six extant geographical subspecies of this species, two of which occur in the study area. The southernmost subspecies, *C. wahlbergi wahlbergi* (Krauss, 1848), occurs from South Africa to southern Tanzania and the second, *C. wahlbergi welwitschi* (Morelet, 1868), in Angola and the Kunene River, but is of doubtful validity (*vide* Mandahl-Barth 1988: 68, fig. 26). Although Appleton (1979) referred to material from the Kunene River as *A. wahlbergi*, he drew attention to the fact that these specimens had a lower L/H ratio (1.75–1.86) than those from other systems to the east (mean for 10 adult specimens from Nseleni River, KwaZulu-Natal, South Africa =2.05 ±0.04, n=10) and thus resembled *C. moutai* recorded from the upper Kunene by Dartevelle (1939). Graf & Cummings (2006) identified the Kunene material examined by them as *C. moutai* (Dartevelle, 1939), but did not record it beyond this system. The absence of this high-shelled *Chambardia* from the upper Zambezi is surprising bearing in mind past, and perhaps present, connections between the upper tributaries of the two (Dudley 2001; Skelton *et al.* 1985). The relationship between *C. wahlbergi* and *C. moutai* in south-central Africa needs critical examination.

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

DISTRIBUTION: South Africa, Botswana*, Malawi, Mozambique, Tanzania and Zimbabwe.

MATERIAL: **Botswana**: Limpopo River, 3 specimens, Stevensford Game Reserve [coordinates unknown], 13.iii.1984, B. van der Waal (UKZN).

NOTES: Formerly referred to as *Aspatharia* (*Spathopsis*) *petersi*, this is a smaller and narrower species than the above, with the dorsal and ventral margins virtually parallel. As far as is known,

C. petersi is restricted to the catchments of the lower Zambezi, Limpopo and Incomati Rivers in Malawi, Zimbabwe, Mozambique and South Africa. The only record from the study area comprises three specimens from the Limpopo River system in north-eastern Botswana. As *C. petersi* is infrequently found, the dimensions of these three specimens are provided here: 68.9 x 31.1 x 19.2 mm, L/H ratio 2.22, umbo at 0.36 length; 64.8 x 27.5 x 16.4 mm, L/H ratio 2.36, umbo at 0.35 length; 62.7 x 27.6 x 16.5 mm, L/H ratio 2.27, umbo at 0.31 length (n=3). These measurements agree with those provided for eight specimens of *C. petersi* from the Zambezi River at Tete, Mozambique, by von Martens (1897) and for a large collection from an Iron Age archaeological site on the banks of the Shingwedzi River, Limpopo Province, South Africa (C.C. Appleton & I. Plug unpubl.) (*vide* Figure 2 below). The L/H ratio of these last mentioned shells decreased as the animal grew, from 2.4–2.6 mm at a valve length of 54–65 mm to 1.95–2.2 mm at a length of 105–125 mm. Over this size range, therefore, the shell becomes narrower at it grows and following the limited data given by von Martens (1897), the umbones move slightly closer to the middle of the valves as valve length increases. The Botswana specimens' valve lengths of 60–70 mm lie in the upper half of the species' size range. As *C. petersi* is a poorly characterised species, the writers include measurements of the material from the Shingwedzi River, South Africa, referred to above. Figure 2 illustrates valve length plotted against maximum height and Figure 3 L/H plotted against length (n=65 in both cases).

Genus: *Mutela* Scopoli, 1777

TYPE SPECIES: *Mytilus dubius*

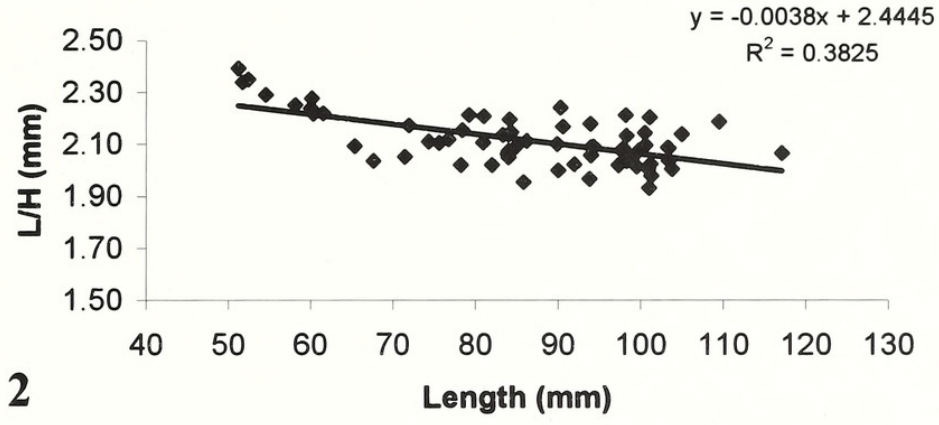
Mutela zambesiensis Mandahl-Barth, 1988

DISTRIBUTION: Angola, Botswana, Namibia, Zambia and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Guma Lagoon (lower panhandle) [SE1822Cd], 12.vi.2000; Moremi Game Reserve, in mud in Gadikwe lagoon [SE1923Aa], 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana**: Okavango Delta, 7 specimens, Thamalakane River bridge, near Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN); 10 specimens, Chief's Island, Nxaraga lagoon [SE1923Ca], 14.iii.1984, C.C. Appleton (UKZN); 1 specimen, Khumaga, Boteti River, in sand and peaty detritus [SE2024Ad], 24.xii.1980, P.E. Reavell (UKZN); 1 specimen, Santantadibe River, 19°34'76"S, 23°22'50"E, 14.xii.1996, E. Taylor (SMN77024) (NMNW); 9 specimens, Gadikwe lagoon [SE1923Aa], vi.2000, C.C. Appleton (UKZN). **Namibia**: Kunene River, 2 specimens, hippo pools below Ruacana Falls [SE1714Ac], 4.x.1987, B.A. Curtis (SMN76508); Namibia: Okavango River, 1 specimen, Shigaya [SE1720dC], 2.xi.1996, B.A. Curtis (SMN76977) (all NMNW). Eastern Caprivi, 3 specimens, Singalamwe [SE1723Cb], [undated], A.C. Evans (SMN76831); 2 specimens, Singalamwe Mulapo [SE1723Cb], Kwando floodplain, 22.x.1987, B.A. Curtis (SMN76564); 2 specimens, Lizauli near Kwando River [SE1823Ab], 15.vi.1982, T.F. Jackson (SMN76832); 1 specimen, Sesheke on Zambezi River [SE1724Ad], [undated], C.J. Schutte (SMN76833); 1 specimen, Zambezi River opposite Lisikili [SE1724Cb], 8.xi.1986, C.H. Schlettwein, N. Lemmer & J. Coetzee (SMN76324) (all NMNW).

TAXONOMIC NOTES: This species is characterised by the very low umbone. As the shell grows, the maximum height (Hmax) moves closer to the posterior end of the shell which gives old shells a distinctly rugose and truncate appearance posteriorly (Figure 4). In this respect they resemble *M. dubia*, as illustrated by Appleton (1979), Daget (1964), and Pilsbry & Bequaert (1927, plate 38). In the series of 90 individuals available from the Okavango Delta and



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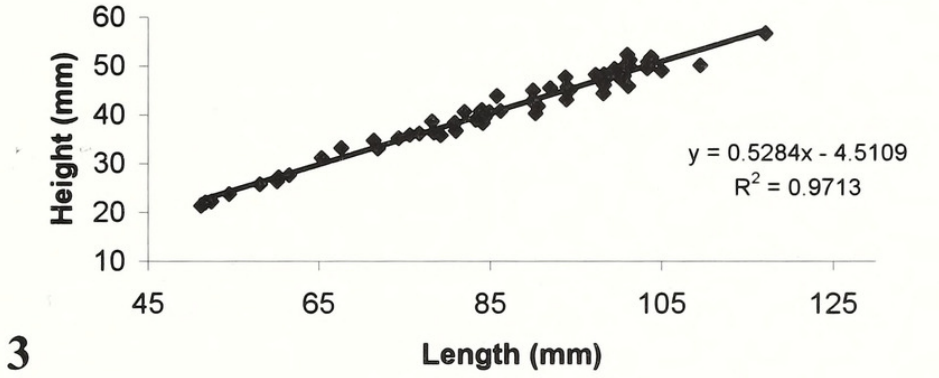

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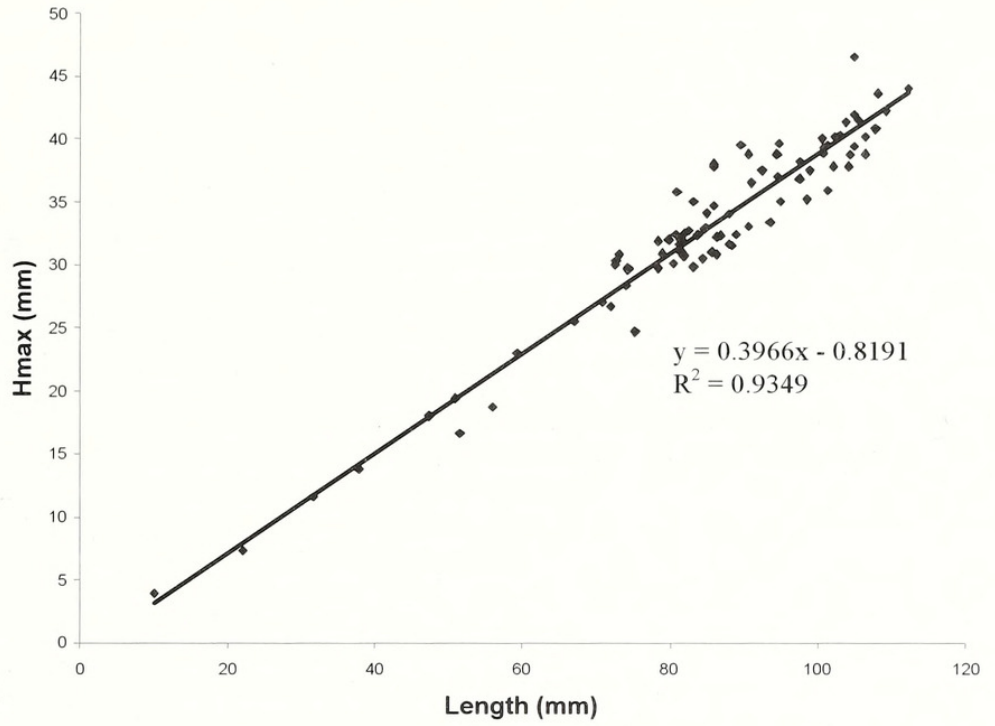
Figure **2–3**. *Chambardia petersi* (von Martens), from the Shingwedzi River, Limpopo Province, South Africa (C.C. Appleton & I. Plug unpubl.). **2**, L/H plotted against L (Y = 0.5284x – 4.5109; R^2 = 0.9713); **3**, H plotted against L (Y = -0.0038X + 2.4445; R^2 = 0.3825)

adjacent eastern Caprivi wetlands, all shells less than 85–90 mm in length resemble *M. rostrata*, while many, but not all of the longer shells resemble *M. dubia*. Blay (1989) and Daget (1964) demonstrate little variation in the shape of the shells of two West African mutelids, *Mutela rostrata* and *Aspatharia sinuata* from geographically separate populations in ecologically different habitats. They argue that this limited between-habitat variability in shell dimensions indicated that the environmental effect is small, resulting in stable shapes that should be considered characteristic for the species. Indeed, Blay (1989) calculated a coefficient of variation of <10% in the mean length:height ratios of shells of both sexes from five widely separate populations of *A. sinuata*. Thus, the differences between the regressions calculated by Daget (1964) for West African species *M. dubia* and *M. rostrata* are taken to reflect characteristic differences in shell length/height relationships. Although he used power curves to describe these relationships, they are very close to straight lines, especially for *M. rostrata*. His equations, solved for shell length (L), are given together below, with L/height (H) and length/width (W) ratios: *M. dubia*: L = 3.715 H0.893; L/H ratio 2.77–3.32; L/W ratio

4.67–6.41. *M. rostrata* (two geographically separate populations combined): L = 3.145 H0.99; L/H ratio 2.65–3.17; L/W ratio 4.63–6.37. The writers therefore follow the above authors in presenting comparable morphometric data for the series of *M. zambesiensis* shells from the Okavango River and Delta, and Linyanti swamps of eastern Caprivi, in an attempt to further characterise this species which appears to be confined to the study area. The best fit linear regression between *M. zambesiensis* shell length (L) and maximum height (Hmax) is given by L = Hmax + 0.8191/0.3966 (L = 0.3966Hmax – 0.8191) (Figure 5) with a correlation coefficient $R^2 = 0.9349$ (n=90). The L/H ratio varied from 2.26 to 3.11, a range which is similar to both *M. rostrata* and *M. dubia*, but the L/W ratio varied between 3.80 and 7.48, which is a broader range than either of these species. The umbones fall between 0.19 and 0.30 (*mean*=0.25) of the length from the anterior end. They were almost always eroded, especially in larger shells, so that their exact position could often only be determined internally. The angles formed by the dorsal/anterior and dorsal/posterior margins were distinct only on shells <85 mm in length, and not in longer ones. The observation by Mandahl-Barth (1988) that as shell size increases, the dorsal margin becomes more sloping, so that Hmax moves closer to the posterior end was confirmed, but only for small and medium-sized shells. Plotting the position of Hmax (expressed as a percentage of total shell length from the posterior end) against shell length (Figure 4) showed that Hmax did move posteriorly, but only in shells up to about 80 mm. When longer shells were included, the relationship could be described by a 2nd order polynomial equation: $Hmax = 0.0029x^2 - 0.4143x + 39.551$ though with a low correlation, $R^2 = 0.2576$ (n=18). For shells longer than ±80 mm, Hmax appears to move anteriorly again, but to differing extents in different individuals. In the two specimens available from the Kunene River (SMN76508), Hmax lay at 0.18 and 0.22 from the posterior end respectively; closer to the posterior end than any from the Okavango system.

NOTES: Mandahl-Barth (1988) 'reluctantly' described *M. zambesiensis* as a new species from the Zambezi River, "... *between Kariba and Chirundu* ...", i.e. downstream of Lake Kariba, Zimbabwe; and from Singalangwe (=Singalamwe), close to the Kwando River in eastern Caprivi, Namibia. It is, in fact, the only species of *Mutela* he recognised from southern Africa. The principal justification for designating the new species was that the southern African shells had features in common with two widespread tropical African species, *M. dubia* (Gmelin, 1791), and *M. rostrata*, but conformed precisely to neither. Younger valves resembled members of Mandahl-Barth's (1988) Rostrata-group of *Mutela* (which includes *M. mabilli*, reported from the study area by Connolly 1931, 1939), whereas older valves were closer to *M. dubia*, which was reported from the study area by Appleton (1979). Curtis (1991) thus recorded both *M. dubia* and *M. rostrata* from the Namibian section of the Kavango River. *Mutela zambesiensis* is known from the Kunene, Okavango (though not commonly from the stretch forming the Namibia/Angola border), and upper Zambezi Rivers, as well as the Chobe/Linyanti system of Eastern Caprivi (Appleton 1979; Appleton *et al.* 2003; Connolly 1931, 1939; Curtis & Appleton 1987; van Bruggen 1980). *Mutela zambesiensis* thus has a south-central African distribution, rather similar to another unionoidan bivalve, *Coelatura kunenensis*. This may be associated with specificity in respect of their fish hosts during their parasitic larval phase, as well as to river capture and changes in river courses in the region in the past. A few specimens of *Mutela* collected in the *lowveld* of Mpumalanga Province, South Africa, may also belong to *zambesiensis* (*vide* Discussion). Van Damme's (1984) statement that *Mutela* reaches its southern limit in Lake Malawi and the Shire River is clearly incorrect.



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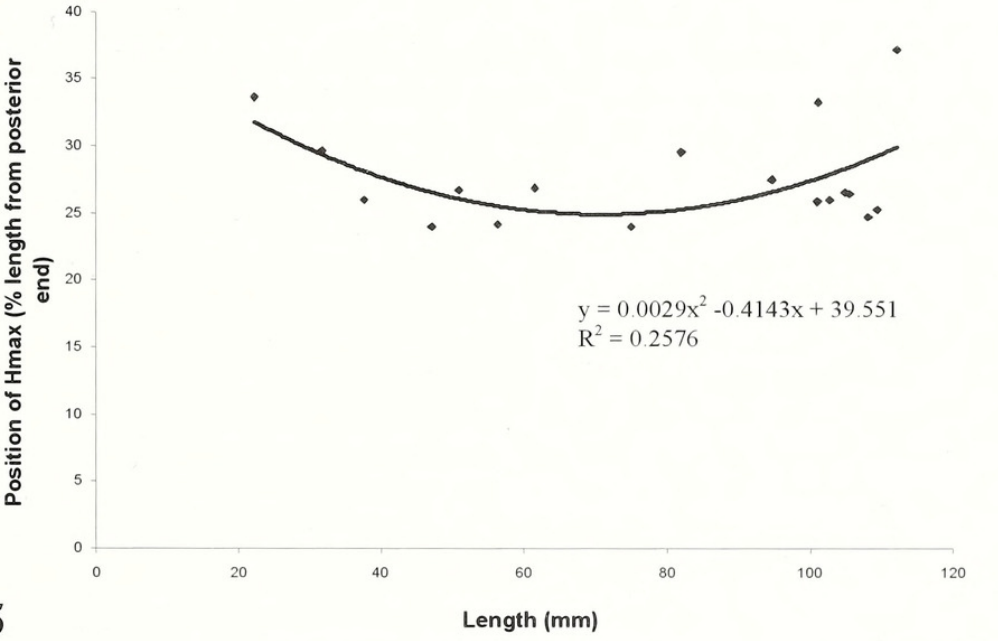

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Figure **4–5**. *Mutela zambesiensis* Mandahl-Barth. **4**, Hmax plotted against L. (Y = 0.3966x – 0.8191; $R^2 = 0.9349$); **5**, position of Hmax on dorsal margin (% length from posterior end) plotted against L. ($Y = 0.0029x^2 - 0.4143x + 39.551$ ($R^2 = 0.2576$).

FAMILY: ETHERIIDAE

Genus: *Etheria* Lamarck, 1807
TYPE SPECIES: *Etheria elliptica*

Etheria elliptica Lamarck, 1807
DISTRIBUTION: Widely distributed in sub-Saharan Africa, including: Angola, Democratic Republic of Congo, Egypt, Ethiopia, Madagascar, Namibia, Nigeria, Senegal, Tanzania, Uganda and Zambia.
MATERIAL: **Namibia**: 1 upper valve, beach at waterfalls below Sera Cafema, 17°09'43"S, 12°08'57"E, 14.xi.2000, K. Schachtschneider (KUN186A) (AMGS). Kunene River, 4 upper valves, immediately below Ruacana Falls [SE1714Ac], 16.xii.1986, B. van der Waal (SMN76834) (NMNW); 3 complete specimens, Croc pool below Ruacana Falls, 17°24'05"S, 14°12'55"E, 11.xi.1997, F.C. de Moor & S. Bethune (KUN6A); 7 upper valves, along banks of floodplain at: 17°02'00"S, 13°28'53"E (site 22 of de Moor *et al.* 2000), 27.xi.1998, F.C. de Moor & S. Bethune (KUN137) (all AMGS).
NOTES: An unmistakeable species, characterised by irregular valves that frequently assumed their shape from the substratum. The lower valve, which may be either the left or right, is cemented to the substratum, usually rock or older shells. The attached valve is the larger and thicker of the two and often exhibits a distinctive lamellate structure, but in the three KUN6A specimens it is flat. The umbo and hinge plate of the upper valve usually protrude over the lower one. The largest of the KUN6A specimens measured 92.1 x 51.5 x 23.0 mm (n=1). Known by the vernacular name 'African river oyster', *E. elliptica* is widely distributed over tropical Africa and Madagascar. In the study area it occurs only in the rapids of the lower Kunene River, i.e. below Ruacana Falls at an altitude of approximately 780 m.a.s.l., as previously reported by Appleton (1979), de Moor *et al.* (2000) and Haas (1936). Curtis (1999) reported large specimens attached to the Calueque-Olushandja Canal, which transfers water from the Kunene River to the Olushandja Dam in north-western Namibia. The Kunene River is the southernmost locality for *E. elliptica*, but the population is threatened by the proposed construction of a second hydroelectric scheme on the Kunene River (*vide* de Moor *et al.* 2000).

SUPERFAMILY: CORBICULOIDEA

FAMILY: CORBICULIDAE

Genus: *Corbicula* von Mühlfeld, 1811
TYPE SPECIES: *Corbicula fluminalis*

Corbicula fluminalis africana (Krauss, 1848) (*Cyrena*)
DISTRIBUTION: Widely distributed in sub-Saharan Africa, including: Botswana, Malawi, Mozambique, Namibia, South Africa and Zimbabwe.
PUBLISHED RECORDS: **Botswana**: Shakawe [SE1821Bd], in sand in the Okavango Delta panhandle, 08.vi.2000 and Moremi Game Reserve [SE1923Ab], Maunachira Channel, 14.vi.20000 (Appleton *et al.* 2003).
MATERIAL: **Botswana**: Okavango Delta, 13 specimens + 3 right valves, Thamalakane River near Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN). **Namibia**: Gariep (Orange) River, 1 specimen + 1 worn left valve, Vioolsdrift [S2817Dc], 16.vii.1980, R. Jubb (UKZN). Kunene River: 2 juveniles, Stein Guard Post, hand-collected off stones in slow current, 17°25'55"S,

13°59'05"E, 12.xi.1997, F.C. de Moor (KUN18G); 1 juvenile, stones-in-current, 17°11'07"S, 13°35'52"E, 16.xi.1997, F.C. de Moor & S. Bethune (KUN48R); 3 juveniles, amongst submerged vegetation (*Hydrostachys polymorpha*) on stones at Otjihandjavero rapids, 17°05'58"S, 13°31'11"E, [undated], F.C. de Moor & S. Bethune (KUN51R); 2 juveniles, at: 17°00'18"S, 13°25'52"E, sediments of pool on floodplain (at site 9 of de Moor *et al.* 2000), 17.xi.1997, F.C. de Moor & S. Bethune (KUN61B) (all AMGS). Okavango River: 1 specimen, shallow water, 24.2 km west of Rundu [SE1719Dc], 29.x.1996, B.A. Curtis (SMN76932); 1 specimen, Kapaku [SE1719Cb], 10.vi.1983, S. Bethune (SMN76836); 1 juvenile, shallow water at: 17°58'63"S, 20°38'32"E, 1.xi.1996, B.A. Curtis (SMN76972) (all NMNW). Eastern Caprivi: 3 specimens, Zambezi floodplain, pool opposite Hippo Island [SE1724Ad], 14.vi.1983, S. Bethune (SMN76835); 1 specimen, Zambezi River, Kalambeza Island [SE1724Da], 5.xi.1986, B.A. Curtis (SMN76280); 3 specimens, Kwando River [locality unknown], [undated], A.C. Evans (SMN76837) (all NMNW).

TAXONOMIC NOTES: Mandahl-Barth (1988) followed Haas (1936) in dividing the many described species of *Corbicula* from Africa into two species-groups: the Fluminalis-group, based on the Asian *C. fluminalis*, and the Astartina-group, restricted to Africa. Three subspecies are recognised in the Fluminalis-group, with the southern African species previously known as *C. africana*, included in *C. fluminalis africana*. The remaining two subspecies occur in East and central African lakes. *Corbicula f. africana* is distributed from the Shaba Province of the Democratic Republic of Congo to South Africa. The remaining species of *Corbicula* known from Africa, *C. astartina*, has not been reported from the study area, although Mandahl-Barth (1968) reported it (as *C. rosini*) from Lake Bangweulu in northern Zambia. *Corbicula fluminalis* should not be confused with another Asian species, the similarly-named *C. fluminea* (Müller, 1774). As far as is known, *C. fluminea* has not been found in Africa, although it has become invasive, reaching pest status elsewhere. The Okavango specimens are relatively small, the largest available measuring 15.0 x 12.2 x 7.9 mm (n=14), and have a distinctly triangular shell. Sculpture is well developed and all shells are olive green/yellow externally, with the internal shell between the pallial line and the umbone pale mauve.

NOTES: In southern Africa, *C. fluminalis* is both widespread and variable and in the study area occurs in all major river systems. It also occurs in the Gariep (Orange) River (Palmer 1996), but there is only one record from the Namibian section. Curtis (1999) reported that *C. fluminalis* had spread from the Kunene River to the Calueque-Olushandja Canal.

FAMILY: SPHAERIIDAE

Genus: *Sphaerium* Scopoli, 1777

TYPE SPECIES: *Tellina cornea*

NOTES: Since both *Sphaerium capense* and *S. incomitatum* often occur sympatrically in the same habitats, detailed descriptions of the shells of these species were provided by Appleton (1996, 2002). Both species have been collected in the Okavango system, but neither has been found in the Kunene River.

Sphaerium capense (Krauss, 1848) (*Cyclas*)

DISTRIBUTION: Botswana, Madagascar, Namibia, South Africa, Zambia and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Guma Lagoon, in sediment-filled crevices between culms of *Cyperus papyrus*, exposed sandy shoreline and permanent small lagoon, between Guma and

Nqoga Channel [SE1822Cd], 11–12.vi.2000; Gadikwe Lagoon [SE1923Aa], 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana**: Okavango Delta, 1 specimen, Boro River [SE1922Bd], 15.xii.1996, B.A. Curtis (SMN77035); 2 specimens, rainfilled backwater at: 19°37'94"S, 20°24'44"E, 13.xii.1996, E. Taylor (SMN77001) (all NMNW). **Namibia**: Kavango River, 5 specimens, small muddy pool, backwater at Cuito confluence below malaria camp at Katere [SE1820Bb], 3.xi.1996, B.A. Curtis (SMN76983) (all NMNW). Eastern Caprivi: 3 specimens, Kwando River floodplain, [locality unknown], [undated], C.D. Dettman (SMN76838); 4 specimens, pools in Kwando floodplain near Sietwa Camp, [SE1823Ab], 18.x.1987, B.A. Curtis & A.C. Evans (SMN76527a) (all NMNW).

NOTES: Shells generally cream/white in colour, but some are dull brown. Widely distributed over southern Africa, from Zambia to South Africa and Madagascar; often occurring in large numbers and sometimes together with the following species, *S. incomitatum*. Connolly (1931) recorded *S. capense* from two localities in Namibia, Grootfontein in the north-east and Seeheim in the south, both far from the present records. The type locality is the Knysna River on the southern coastal strip of South Africa, where the species was noted by Krauss to be common (*vide* Herbert & Warén 1999, as *Cyclas capensis*). The type locality may, however, be erroneous, as it has not been reported from the area since and although Krauss undoubtedly collected freshwater molluscs in the Knysna River (*vide* Herbert & Warén 1999), he also collected extensively in the environs of Durban, a more acceptable locality (*vide* entry for *Eupera ferruginea*).

Sphaerium incomitatum (Kuiper, 1966a) (*Pisidium*)

DISTRIBUTION: Botswana, Democratic Republic of Congo, Namibia, South Africa, Zambia and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Guma Lagoon (sandy shoreline) and mud in small lagoon between Guma and Nqoga Channel [SE1822Cd], 12.vi.2000; Gadikwe Lagoon [SE1923Aa], 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana**: Okavango Delta, 3 specimens, Boro River [SE1922Bd], 15.xii.1996, B.A. Curtis (SMN77035) (all NMNW). **Namibia**: Okavango River, 1 specimen, south bank, sandy substratum at: 17°56'96"S, 21°04'99"E, 3.xi.1996, B.A. Curtis (SMN76979) (NMNW). Eastern Caprivi: 1 specimen, Kwando floodplain [locality unknown], [undated], C.D. Dettman (SMN76839); 6 specimens, pools in Kwando floodplain near Sietwa Camp [SE1823Ab], 18.x.1987, B.A. Curtis & A.C. Evans (SMN76527b) (all NMNW).

NOTES: As with the preceding species, *S. incomitatum* is distributed over southern and south-central Africa, from South Africa to northern Zambia and Shaba Province of the Democratic Republic of Congo.

Genus: *Pisidium* C. Pfeiffer, 1821

TYPE SPECIES: *Tellina amnica*

Pisidium ovampicum Ancey, 1890 (*Pisidium*)

DISTRIBUTION: Ethiopia, Kenya, Madagascar, Namibia, South Africa and Uganda.

NOTES: The type locality of this species, Omambonde [Okambonde 1716Cc or Omubonde 1714Ad] in Ovambo, Namibia (Connolly 1931, 1939; Kuiper 1964, 1966a), remains the only record for the study area. It is, however, 'vague' (Connolly 1931) and cannot be precisely

located, although it is possibly a Herero name. Connolly (1931) commented, as did Mandahl-Barth (1988), that this species with its rounded shape and almost centrally-placed umbones closely resembled small examples of the genus *Sphaerium*. Mandahl-Barth (1988) listed the "... *poor size and, as a rule, the white shell* ..." as characters of *P. ovampicum* that distinguish it from juvenile *Sphaerium* of the same size, although it is not clear what he exactly meant by 'poor size'. The species is distributed from South Africa to Ethiopia and Madagascar.

Pisidium casertanum (Poli, 1791) (*Cardium*)

DISTRIBUTION: Widely distributed across Africa, including: Canary Is., Ethiopia, Kenya, Madagascar, Madeira Is., Namibia, Rwanda, South Africa, Sudan, Tanzania, Uganda and Zimbabwe.

NOTES: A species described from Europe, but widely distributed in Africa from South Africa to Ethiopia and north-west Africa. The only locality in the study area is a single record from Grootfontein, Namibia (Kuiper 1964, 1966a). Mandahl-Barth (1988) noted that this is the most enigmatic of the African *Pisidium* spp., as it lacks any clear distinguishing features.

Pisidium langleyanum Melvill & Ponsonby, 1891 (*Pisidium*)

DISTRIBUTION: Lesotho, Namibia, South Africa and Zambia.

MATERIAL: **Namibia**: 4 specimens, marshy area below dam on farm Strydfontein [SE1918Ca], 3.ix.1988, B.A. Curtis (SMN76625); 2 specimens, spring on farm Spitzkop [SE1918Ac], 5.ix.1988, B.A. Curtis (SMN76639) (all NMNW).

NOTES: In the study area this species is only known from Namibia, and only from isolated waterbodies on two farms in the Grootfontein District. It has not been collected from any natural watercourses. There is no thickening (='nodule' of Mandahl-Barth 1988), at the anterior end of the posterior lateral tooth (p3) in the right valve. The presence of such a nodule is diagnostic for the similar species, *P. viridarium* (*vide infra*). *Pisidium langleyanum* is restricted to southern Africa, from South Africa to northern Zambia.

Pisidium viridarium Kuiper, 1956 (*Pisidium*)

DISTRIBUTION: Widely distributed across southern and central Africa, including: Botswana*, Democratic Republic of Congo, Ethiopia, Kenya, Lesotho, Madagascar, Rwanda, South Africa, Uganda and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Okavango Delta, Moremi Game Reserve Reserve [SE1923Ab], in sediments of slowly-flowing Maunachira Channel, 14.vi.2000 (as *Pisidium* sp., Appleton *et al.* 2003).

MATERIAL: **Botswana**: Okavango Delta, 5 valves, Nxaraga Lagoon, Chief's Island [SE1923Ca], in mud amongst vegetation in shallow water, iii 1984, C.C. Appleton (UKZN).

NOTES: Conspicuous ferruginous deposits are present on the posterior and dorsal parts of the shells, corresponding to those aspects that protrude from the substratum when the live animal is partially buried. Recent collecting (H. Dallas pers. comm. 2004), has shown *P. viridarium* to occur more widely in the Moremi area of the Delta than the above records indicate. It is distributed from South Africa to Kenya.

TAXONOMIC NOTES: Mandahl-Barth (1988) followed Kuiper (1964, 1966a), in noting that *P. viridarium* is closely allied to the central African species *P. kenianum*, but may be separated from the latter on the basis of a small nodule in front of the posterior lateral tooth (p3) in the right valve. Mandahl-Barth (1988) went further and proposed that *P. kenianum* is a northerly race of the southern African *P. langleyanum*. Until these questions have been clarified, the writers retain the name *viridarium* for the most common *Pisidium* in the Okavango Delta.

Pisidium (*Parapisidium*) *reticulatum* Kuiper, 1966b

DISTRIBUTION: Botswana*, Madagascar, Malawi and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Okavango Delta, Moremi Game Reserve [SE1923Ab], from sediments at the margin of the Maunachira Channel, 14.vi.2000, [C. Appleton & B. Curtis] (Appleton *et al.* 2003).

NOTES: A little known, but unmistakable species, described from material collected in the Gwebi River, Zimbabwe, and from Nossi-Bé Island [=Nosy Be], Madagascar. Mandahl-Barth (1988) cites an additional record from the southern part of Lake Malawi. The single specimen from Botswana (cited above) was collected together with *Corbicula fluminalis*, *Eupera parasitica* and *P. viridarium* (Appleton *et al.* 2003).

TAXONOMIC NOTES: Recognised by its external ligament and unique reticulate sculpture. The only other southern African *Pisidium* with an external ligament is the widespread species *P. pirothi*. Figures 6–8 illustrate three aspects of paratype No. 4 of *P. reticulatum* collected in Nossi-Bé Island, Madagascar, by F. Starmühlner in 1958, housed in NMSA (L5669/T1799).

Genus: *Eupera* Bourguignat, 1854

TYPE SPECIES: *Pisidium moquinianum*

NOTES: On the basis of their original descriptions, the two species of *Eupera* reported from southern Africa, namely: *E. ferruginea* and *E. parasitica*, are separable on shell shape and sculpture. Mandahl-Barth (1988) did not recognise *E. parasitica*, however, and included this as a synonym of *E. ferruginea*. Both species names are applied here, but it is noted that a revision of the African species of the genus is required (*vide infra*).

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

DISTRIBUTION: Widely distributed across Africa, including: Botswana, Egypt, Ethiopia, Madagascar, Mauritius Is., Mozambique, Namibia and South Africa.

PUBLISHED RECORDS: **Botswana**: Okavango River, upper panhandle [SE1821Bd], 7–8.vi.2000 [C. Appleton & B. Curtis] (Appleton *et al.* 2003).

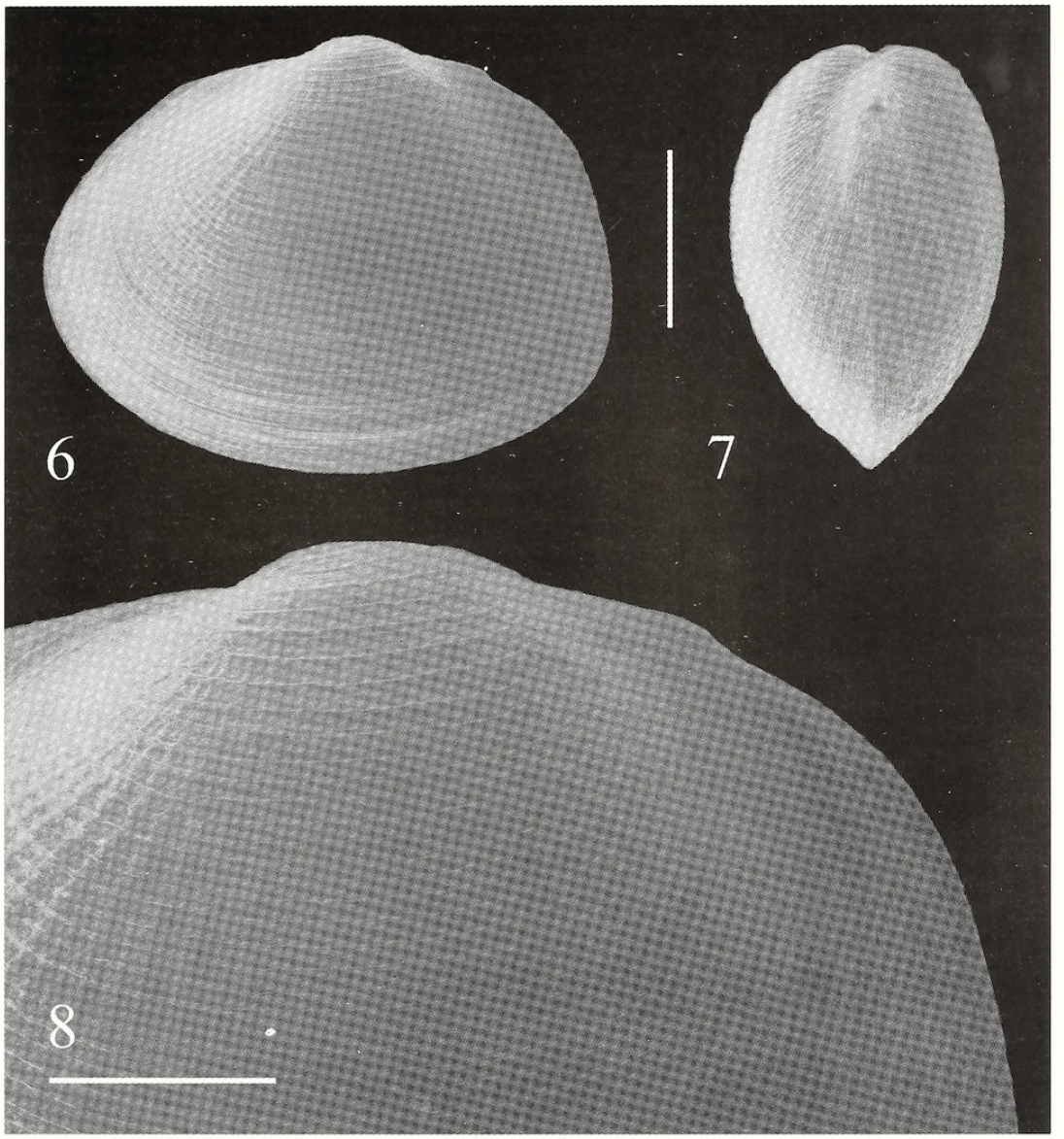
MATERIAL: **Botswana**: Okavango Delta, 1 empty specimen, Okavango Delta panhandle at Shakawe [SE1821Bd], 10.xii.1996, B.A. Curtis (SMN76994) (NMNW). **Namibia**: Okavango River, 1 specimen, Popa Falls [SE1821Ba], 21.x.1984, S. Bethune (SMN76108b); 1 specimen, same except: 14.xi.1983 (SMN76412) (both NMNW). Eastern Caprivi: 7 specimens, pools in Kwando floodplain near Sietwa Camp [SE1823Ab], 18.x.1987, B.A. Curtis & A.C. Evans (SMN76524) (all NMNW).

NOTES: *Eupera ferruginea* has a pan-African distribution, from South Africa to Egypt, but in the study area has only been collected in the Okavango system and the Eastern Caprivi wetlands. It is found in a variety of habitat types: out-of-current stream sediments, between rocks in rapids, such as Popa Falls on the Okavango River and silt-filled crevices between *Cyperus papyrus* culms. As in *Sphaerium capense*, the type locality of this species is the Knysna River, South Africa, but it has not been collected since in that area and may be an error (*vide* Herbert & Warén 1999, as *Cyclas ferruginea*). The discussion under *S. capense* also applies to this species.

Eupera parasitica (Deshayes, 1854) (*Pisum*)

DISTRIBUTION: Botswana, Egypt, Namibia* and Uganda.

PUBLISHED RECORDS: **Botswana**: Moremi Game Reserve [SE1923Ab], from sediments at the margin of the Maunachira Channel, 14.vi.2000, [C. Appleton & B. Curtis] (Appleton *et al.* 2003).



Figures **6–8**. SEM micrograph of *Pisidium reticulatum* Kuiper (paratype No. 4, NMSA). **6**, left valve; **7**, posterior aspect, indicating moderate inflation of closed valves; **8**, detail of sculpture and external ligament. Scale bars: 6 & 7 = 1 mm; 8 = 500 μm.

MATERIAL: **Namibia**: Kunene River, 1 specimen, Stein Guard Post, riffle, 17°25'55"S, 13°59'05"E, 12.xi.1997, F.C. de Moor & S. Bethune (KUN16F); 7 specimens, same except: hand-collected off stones in slow current, 12.xi.1997, F.C. de Moor (KUN18F) (AMGS).

TAXONOMIC NOTES: Similar to *E. ferruginea*, but differing in the following respects: *E. ferruginea* has the valves relatively higher and shorter than in *E. parasitica*; *E. ferruginea* has 8–14 growth

Table 1. Occurrence of bivalve species in the seven major river and wetland systems of Botswana and Namibia.

Genus & species	Kunene River	Okavango River	Okavango Delta	Eastern Caprivi wetlands	Upper Zambezi River	Limpopo River	Gariep (Orange) River
Aspatharia pfeifferiana	+	+	+		+		
Coelatura kunenensis	+	+	+	+	+		
C. mossambicensis						+	
Corbicula fluminalis	+	+	+	+	+		+
Etheria elliptica	+						
Eupera ferruginea		+	+	+			
E. parasitica	+		+				
Mutela zambesiensis	+	+	+	+	+		
Pisidium reticulatum			+				
P. viridarium			+				
Chambardia petersi						+	
C. wahlbergi	+	+					
Sphaerium capense		+	+	+			
S. incomitatum		+	+	+			
Unio caffer							+
Total no. of species	**7**	**8**	**10**	**6**	**4**	**2**	**2**

lines per millimetre (measured in the middle of a valve), whereas *E. parasitica* has 14–16 (Appleton 2002). The KUN specimens (listed above) have 15–24 (*mean*=20) growth lines/mm and the largest specimen measures 4.1 x 3.0 x 1.9 mm. Only one of these Kunene shells has a pattern of radiating dark flecks, usually apparent in the genus in other river systems (e.g. the Okavango system); the remainder are all uniform cream/yellow. Although such uniform pale colouration has not (to our knowledge) been previously noted in southern Africa, Mandahl-Barth (1954), does note this character in both his generic and species descriptions. Mandahl-Barth (1988) later regarded *E. parasitica* to be a synonym of *E. ferruginea*. There is thus debate over the taxonomic position of this species which, if it is considered valid, is distributed over eastern and northern Africa. These are the first records from southern Africa. The name *parasitica* may relate to the way *Eupera* uses its byssus threads to attach to submerged surfaces such as vegetation (Appleton 1977), or cavities in *Etheria* valves (Pilsbry & Bequaert 1927).

DISCUSSION

A total of 18 species of freshwater bivalve has been reported from Botswana and Namibia. In most cases these are well-described, but some revision may be necessary in respect to the four species and/or genera: *Coelatura kunenensis*, *Eupera*, *Mutela zambesiensis* and *Pisidium*. Appleton's (1979) morphological comparison of *Coelatura* from the Kunene, upper Zambezi and Kafue Rivers, on the one hand, and the Okavango

system on the other, should be extended and pan-African reviews of *Eupera* and *Pisidium* are also desirable.

New morphometric data are presented for *Mutela zambesiensis* and *Spathopsis petersi*. The latter is uncommon and the published description of the former is brief; Mandahl-Barth (1988) noting that is requires better characterisation. The additions to the description of *M. zambesiensis* are based on the study of the morphometry of a West African iridinid, *Aspatharia sinuata*, by Blay (1989). Blay demonstrates a coefficient of variability of <10% in the mean length:height ratios of shells of both sexes and different sizes from five widely separated habitats in Nigeria, three lotic and two lentic. He interpreted this limited between-habitat variability in shell dimensions as indicating a relatively small environmental effect on an otherwise stable shell form for the species. Assuming this to apply to other Iridinidae, the H *vs.* L regression equations provided by Daget (1962, 1964), for West African species of *Aspatharia* and *Mutela* respectively, may be useful in separating several species of the two genera, and hence, in defining *M. zambesiensis*. This is somewhat at variance with the widely held view that habitat diversity and instability have, by promoting reproductive isolation, led to variation in shell form in freshwater molluscs at the subspecific or variety level, but are too short-term to have resulted in speciation. It could be argued, however, that such intraspecific variability is more likely to be a characteristic of pulmonate gastropods than of bivalves, as the former have colonised a greater range of habitat types over a wider geographical area and have much shorter generation times.

In terms of diversity, the bivalve fauna of the northern areas of Namibia and Botswana is a rich one. This is probably because, as noted earlier, the drainages involved extend into central Africa and abut the species-rich Zaïre system. Table 1 illustrates the

Table 2. Bivalve species reported from south-central Africa, arranged in three categories, based on known distribution patterns. These categories differ from those used for the gastropods of the Okavango system by Brown *et al.* (1992).

1. Species widely distributed in tropical/sub-tropical Africa (50%)	**2.** Species distributed in southern and south-eastern Africa (39%)	**3.** Species confined to south-central Africa (11%)
Aspatharia pfeifferiana *Corbicula fluminalis* *Etheria elliptica* *Eupera ferruginea* *E. parasitica* *Pisidium casertanum* *P. ovampicum* *Chambardia wahlbergi* *Sphaerium capense*	*Chambardia petersi* *Coelatura mossambicensis* *Pisidium langleyanum* *P. reticulatum* *P. viridarium* *Sphaerium incomitatum* *Unio caffer*	*Coelatura kunenensis* *Mutela zambesiensis*

occurrence of 15 species in the seven major river/wetland systems in Namibia and Botswana. The other three species, *Pisidium casertanum*, *P. langleyanum* and *P. ovampicum*, have only been sampled from isolated marshes and springs in the interior of Namibia.

The Okavango River and Delta support the greatest diversity, with eight and 10 species respectively, including three species of Sphaeriidae in the former and six in the latter. These tiny bivalves are best collected from sieved sediment samples, but as far as the writers are aware, this has only been undertaken in the Okavango Delta. Indeed, the finding of three sphaeriid species occurring sympatrically in the sediments at one station on a slowly-flowing channel in the Okavango Delta (Appleton *et al.* 2003), is evidence that they are more common in the area than previously thought. Neither *A. pfeifferiana* nor *C. wahlbergi* is widespread in the study area, but the absence of the latter from the Okavango Delta and upper Zambezi, and the former from the Eastern Caprivi wetlands, may simply reflect inadequate sampling in these systems. The presence of the river oyster *E. elliptica* only in the Kunene is, however, likely to be true, as the rapids and waterfalls that constitute its habitat are uncommon in the other rivers. With these points in mind, it is useful to note that Brown *et al.* (1992) reported five gastropod species as occurring in the Okavango River, but not in the Okavango Delta. That number has since declined to two with the finding of *Bulinus tropicus*, *Melanoides victoriae* and *Segmentorbis kanisaensis* in the Delta by Curtis (1997) and Appleton *et al.* (2003).

With the exception of *Pisidium casertanum*, *P. langleyanum*, *P. ovampicum* and *Unio caffer*, the species here constitute a largely tropical assemblage, concentrated in the rivers systems forming the northern borders of the two countries, *viz.* the Kunene, Okavango and Zambezi systems. One species, the river oyster, *Etheria elliptica*, reaches the most southerly limit of its range in the Kunene River on the Namibia/Angola border, while two others, *Aspatharia pfeifferiana* and *Coelatura kunenensis*, do so in the Okavango Delta in Botswana. Neither occurs in south-eastern Africa, although *A. pfeifferiana* was reported from Zimbabwe by Connolly (1939). *Mutela zambesiensis* occurs in all three large river systems in the study area, and small samples of *Mutela* collected by C.H.J. Schutte in the 1970s and the late A.C. Evans in 1988 in the *lowveld* of Mpumalanga Province, South Africa, suggest that it may be distributed more widely across the sub-continent. Until recently the only localities where *Pisidium* had been recorded were isolated springs in the Grootfontein District of Namibia, but the finding of two species in the Okavango Delta (Appleton *et al.* 2003), indicates that these small bivalves are more generally distributed and future collecting should target them. Kuiper (1965) described a new species of bivalve, *Micranodonta regii* (family not established), from the Waterberg area of north-eastern Namibia, but this was a misidentification. The shells illustrated are those of a conchostracan crustacean belonging to the family Cyzicidae, probably *Caenestheriella australis* (Lóven, 1847) (M.L. Hamer pers. comm. 1997).

The zoogeographical affinities of the freshwater bivalve fauna of Namibia and Botswana appear to reflect three components (Table 2). These being 1) a tropical/subtropical African component, including species distributed widely across tropical and sub-tropical Africa and occurring in the Zaïre River system immediately to the north of the study area; 2) a southern and south-eastern African component; and 3) a small regional 'south-central African' component.

Less than half (44%) of the species recorded from the study area also occur immediately to the north, in the Lake Bangweulu-Luapula River basin in northern Zambia (Mandahl-Barth 1968). This list includes only three of the eight unionoidan bivalves listed in Table 2, *A. pfeifferiana*, *C. wahlbergi* and *E. elliptica*, which for the two iridinids may reflect the dispersal of their host fish during their parasitic larval phase. It is not known whether *E. elliptica* has a parasitic larva. Furthermore, six of the species present in the Bangweulu-Luapula system are categorised as 'tropical/sub-tropical African species' in Table 2, three as 'southern African species', at the northern limit of their ranges, but none as south-central African endemics. The three species in category 1 not found in this adjoining system are all sphaeriids which are, as noted above, small and often missed.

Endemism among bivalves is low in the study area, i.e. only the two unionoidan species constituting category 3 above, especially when compared to the Zaïre River basin, in which Dudley (2001), estimated there are 14 endemic species. It may be no coincidence that these two are both in need of taxonomic revision, and that one, *M. zambesiensis*, may extend into eastern South Africa. It is tempting to attribute the restriction of *C. kunenensis* and *M. zambesiensis* in south-central Africa to fish host-specificity, resulting in fewer opportunities for dispersal. However evidence from a study of the reproductive biology of unionoidan bivalves from Lake Kariba (Kenmuir 1980a, 1980b, 1980c) suggests, both from experiments and field catches, that these bivalves may not be rigidly host-specific and may use a variety of fish species as hosts. Most of these belong to the family Cichlidae. *Mutela zambesiensis* also develops on a mormyrid. An exception may be *C. wahlbergi*, which failed to develop on several cichlid species or on *Barbus* sp. (Cyprinidae). This led Kenmuir (1980a) to suggest that *C. wahlbergi* may be more host-specific than other species. This may have implications for its dispersal and may explain its limited distribution in the study area (Table 1).

The fish fauna of the Okavango system is similar, in terms of species present, to those of the adjacent upper Zambezi and Kunene river systems, sharing 96% and 54% of species with these systems respectively (Skelton *et al.* 1985). In addition, all the species cited by Kenmuir (1980a) as hosts for larval *C. mossambicensis* and *M. zambesiensis* in Lake Kariba are also widespread in the Okavango. This similarity may be explained by links that either exist today, or have done in the past, between the Okavango and other river systems in the region. Very tenuous links exist across hundreds of kilometres of

currently dry terrain between the Okavango and the Kunene *via* the Cuvelai drainage and with the upper Zambezi *via* the Selinda Spillway and Eastern Caprivi wetlands (Skelton *et al.* 1985). More substantial links existed between these systems in the past and also between the Okavango and Limpopo and Gariep (Orange) rivers. A valuable discussion of the past links between the river systems in the study area was provided by Dudley (2001), and may be summarised by his concluding comment that '... *during the Pleistocene, extensive parts of the central African plateau were connected hydrologically and wetland organisms had an easy means of dispersal across them.*'

A zoogeographical map of Africa based on freshwater mollusc distribution (van Damme 1984), shows the study area occupying most of the western and central parts of the 'Angola-Zambesian' district of the 'South African Province', which in turn forms part of the 'East & South African Subregion'. As with Dudley's (2001) review, this draws attention to the fact that the Kunene-Okavango and Zambezi basins form a 'cross-way' of fresh waters running from west to east across the continent. This conduit provided access to the sub-tropical lowlands of south-eastern Africa and may account for the low endemicity among bivalves in the study area.

Distribution patterns may change however. Curtis (1999) has provided important evidence that two species, *Corbicula fluminalis* and *Etheria elliptica*, have been introduced from the Kunene River into the Calueque-Olushandja canal in north-west Namibia, and *C. fluminalis* into the associated oshanas and the Cuvelai basin as well. *Coelatura kunenensis* also occurs in these oshanas. This is significant because it suggests that the predicted translocation of molluscs *via* the system of inter-catchment canals being built in northern Namibia from both the Kunene and Okavango rivers to dams in the country's interior (Bethune 1985; Bethune & Chivell 1985) has become a reality.

Whether *C. kunenensis* occurs naturally in these oshanas is not clear, but van der Bank (1995) showed using enzyme electrophoresis that this species (from the Zambezi River above the Victoria Falls) had a heterozygosity value (H) of 7.5%; the first such measurement for any African bivalve species. The author noted that H=7.5% was relatively low compared with data from non-African freshwater bivalve populations and may be a consequence of the inherent instability of African riverine habitats and those associated with rivers, e.g. the oshanas where Curtis (1999) collected *C. kunenensis*. The restoration of populations after periods of drought or flood will rely on immigration from refugia within the system, or reproduction by residual founder populations, and this could create recurrent genetic bottlenecks that would be compatible with this finding.

Little is known of the biology or ecology of freshwater bivalves in southern Africa. Kenmuir (1980a, 1980b, 1980c) provided unique data on the standing stocks and reproductive biology of three unionacean species (*Chambardia wahlbergi*, *Coelatura mossambicensis* and *Mutela zambesiensis*) in Lake Kariba, Zimbabwe. Although bivalves can become the dominant members of the benthos of freshwater habitats, they are

sedentary animals and are thus severely affected by droughts when water levels drop. Some, such as *C. wahlbergi*, are able to survive periods of desiccation of up to 2½ years (Cockson 1971), but many die during droughts. Such large-scale drought-related mortalities allowed Marshall (1975) and Appleton & la Hausse de Lalouviere (1987) to measure the population densities of *Coelatura framesi*, *C. mossambicensis*, *C. wahlbergi*, *Corbicula fluminalis* and *M. zambesiensis* in the exposed sediments of Lake Chivero (formerly Lake McIlwaine) in Zimbabwe and the Pongolo River floodplain in South Africa. Appleton *et al.* (2003) presented data on the population densities of *C. kunenensis*, *M. zambesiensis* and *C. fluminalis* in the Okavango Delta, relative to the grain size composition of the sediments in which they were living.

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