

Freshwater molluscs of the Eastern Congo: notes on taxonomy, biogeography and conservation

Roland Schultheiß¹*, Oscar Wembo Ndeo², Meni Malikwisha², Carina Marek¹, Ulrich Bößneck¹ and Christian Albrecht¹

¹Department of Animal Ecology & Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32 (IFZ), Giessen, 35392 Germany; roland.schultheiss@bio.uni-giessen.de, carina.marek@allzool.bio.uni-giessen.de, uboessneck@aol.com, christian.albrecht@allzool.bio.uni-giessen.de

²Ruwenzori State University, BP 560 Butembo, D. R. Congo; wemboscar@yahoo.fr, menimalik@yahoo.fr

*Author for correspondence

ABSTRACT

The freshwater habitats of the Eastern Congo are among the least investigated areas on the African continent. This severely restricts our understanding of the composition and distribution of the gastropod and bivalve communities in this region. This lack of knowledge, in combination with very limited recent collections, hampers the phylogenetic assessment of several molluscan taxa on the Pan-African scale and conservation efforts targeting this most prominent taxon of the macrozoobenthos. We here report on species obtained in the Eastern Congo in 2010. In total, 20 gastropod and bivalve taxa were collected from 24 freshwater habitats of the Nile and the Congo drainage system. By compiling faunal and taxonomic data we also aim to provide information of relevance to conservation efforts.

KEY WORDS: Gastropoda, Bivalvia, Congo, Nile, Semliki, Ituri rainforest, Lake Edward, conservation.

INTRODUCTION

The East African Rift system is a well-known hotspot of freshwater biodiversity. The rift lakes within this system are often millions of years old and harbour several hundred species, the most famous ones probably being the endemic cichlid fish and mollusc taxa (e.g., Williamson 1981; Wilson *et al.* 2004; Seehausen 2006; Genner *et al.* 2007a). Slightly west of Lake Edward, however, is a less acknowledged yet equally important biogeographical feature: the water divide that separates the drainage of the Nile from the drainage of the Congo River (Fig. 1). Four major freshwater ecoregions are described from this part of Africa (Abell *et al.* 2008; Fig. 1): (I) The Albertine Highlands ecoregion has a tropical, wet climate and is characterized by rivers and streams connected to the Lualaba River; (II) The Cuvette Central ecoregion has an equatorial wet climate and consists of moist forest rivers. Its main characteristic features are the Congo River and lowland tropical rainforest; (III) The Upper Nile ecoregion, encompassing the tributaries of the White Nile such as the Semliki River and having a subequatorial climate in its southern part (Thieme *et al.* 2005); (IV) Lake Edward belongs to the Victoria Basin ecoregion, which is characterized by large lakes and has an equatorial climate.

The Congo and the Nile river systems harbour highly diverse yet very different mollusc faunas (Van Damme & Van Bocxlaer 2009). Whereas the freshwater molluscs east of the Congo–Nile divide have been studied intensively over the past decades, very little is known of the taxa west of the divide. Since the early work of Pilsbry and Bequaert (1927) on the Congo's freshwater molluscan fauna, malacological sampling has been carried out very rarely in the eastern region of the country in general and in the Ituri rainforest in particular (but see Baluku *et al.* 1989; Chartier *et al.* 1992). The most recent account of freshwater molluscs of Central Africa (Graf *et al.* 2011: 61) states: "Many ...

species in the region are known from only a relatively small number of specimens, and most of those have not been corroborated by recent collecting.” For the entire Congo basin, new material of selected molluscan groups has been studied only occasionally and has often originated from very restricted regions (e.g., Appleton 1979; Piechocki 1993; Piechocki & Korniuschin 1994). Most of the literature focuses exclusively on intermediate gastropod hosts of medically relevant parasites (e.g., Frandsen *et al.* 1978; Loreau & Baluku 1987; Baluku *et al.* 1989; Chartier *et al.* 1990*a, b*, 1993). Hence, modern phylogenetic evaluations are largely absent for this region and the lack of such studies hampers discussions on the origin and biogeographical relationships of African Mollusca (e.g., Michel *et al.* 1992; Van Damme & Pickford 2003; Wilson *et al.* 2004; Glaubrecht & Strong 2007; Glaubrecht 2008).

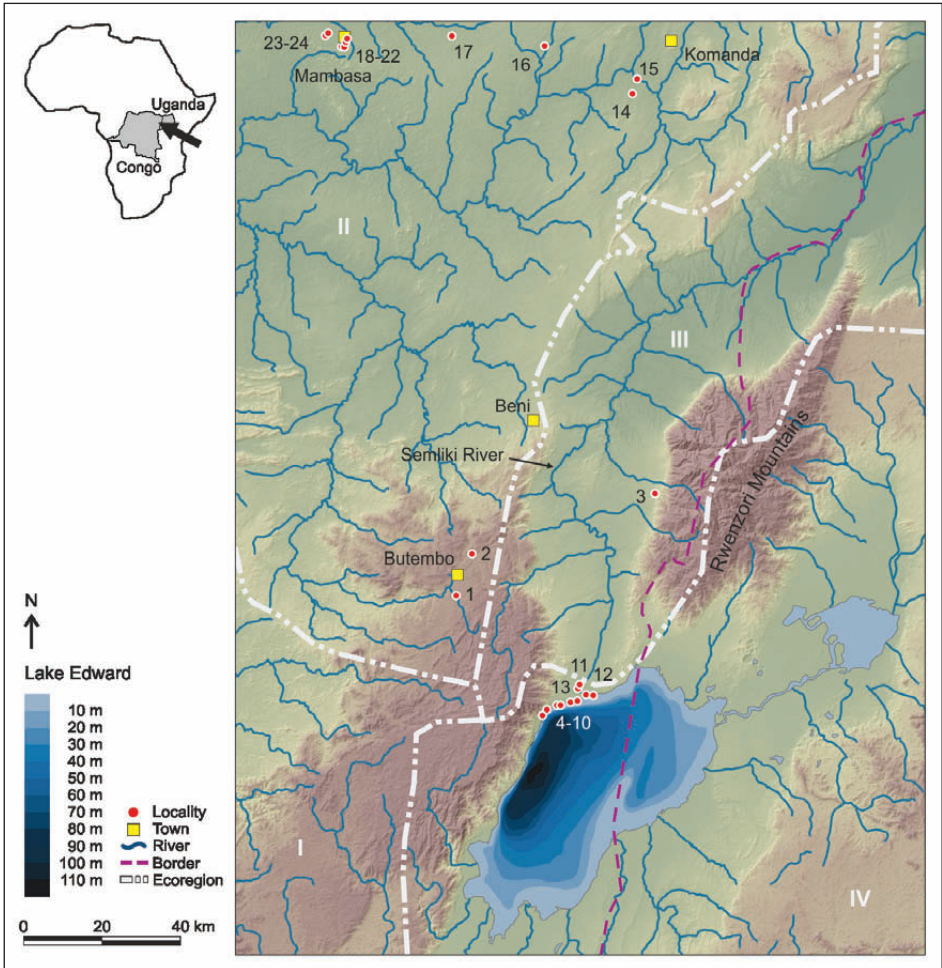


Fig. 1. Map of the investigated area. The purple dashed line indicates the border between the D. R. Congo (left hand side) and Uganda. Freshwater ecoregions (Abell *et al.* 2008) are separated by a light grey dashed line: I – Albertine Highlands, II – Cuvette Central, III – Upper Nile, IV – Lake Victoria Basin. The Congo-Nile water divide follows the borders between ecoregion II and III as well as between I and IV. Red dots mark collecting localities; larger towns and cities are indicated by yellow squares.

The freshwater fauna of large parts of Central Africa has experienced considerable anthropogenic pressure due to deforestation, mining and untreated wastewaters (Thieme *et al.* 2005). Furthermore, recent conservation efforts have been hampered by a lack of public acceptance: although gastropods and bivalves represent a critical subset of limnic biodiversity and are the most prominent group of the macrozoobenthos, “the unique molluscan diversity of the region is fully appreciated by neither the relevant governments nor indigenous communities” (Graf *et al.* 2011: 59). Moreover, the conservation status of many freshwater molluscs from this region cannot be assessed adequately due to insufficient data.

We here report on molluscan taxa collected during fieldwork in the Eastern Congo in 2010 and comment on habitat characteristics as well as on species distributions. Therewith, we aim to provide faunal information with relevance to conservation efforts.

MATERIAL AND METHODS

Gastropod and bivalve species were collected in March and April 2010 in riverine and lacustrine habitats in the Provinces Orientale and North-Kivu (Democratic Republic of the Congo; Fig. 1) by RS, OWN, and MM in the Nile and Congo drainage systems. Sampling was carried out utilizing sieves and a dredge for collecting at greater depths from boats at Lake Edward and the Semliki River.

All specimens were preserved in 80% ethanol and are deposited in the UGSB collection (University Giessen Systematics & Biodiversity collection, Germany). Images were taken using a digital microscope (Keyence VHX-600). Species were determined by RS, CA and UB based on the original literature, if not stated otherwise. Nomenclature largely follows Mandahl-Barth (1988), Brown (1994), Daget (1998), Bouchet & Rocroi (2005), and Bouchet *et al.* (2010). Our use of the qualifier “cf.” follows the recommendation of Bengtson (1988).

Collecting sites for each taxon refer to numbers in Tables 1 and 2 as well as in Fig. 1. Red List Categories of the International Union for Conservation of Nature (IUCN) are provided for each species where available.

TAXONOMY

Gastropoda

Family Ampullariidae Gray, 1824

Pila ovata (Olivier, 1804)

Fig. 2A

Ampullaria ovata: Olivier 1804: 39, pl. 31, fig. 1. (Type locality: “Du lac Maréotis”, Alexandria, Egypt)

Taxonomic remarks: Brown (1994) reports a total of five *Pila* species in Africa (excluding Madagascar). *P. ovata* appears to be the most widespread of them.

Habitat description: We have collected this species in small flowing waters as well as in an irrigation channel with no apparent water movement (Tables 1, 2; Fig. 4H). The main substrate type of the former is clay with detritus and sand, of the latter mostly detritus and sapropel.

Collecting sites: 18, 20, 24.

IUCN Red List Category: Least Concern (Ghamizi *et al.* 2009a).

TABLE 1

Locality information: Numbers in the first row refer to collection sites in the taxonomy section, Table 2, and Fig. 1. Coding: Coll. depth – collecting depth in metres.

#	Province	Locality	Longitude	Latitude	Coll. depth
1	North-Kivu	Mususa River, adjacent fields with irrigation channel	29.28619	00.08781	0.1
2	North-Kivu	Luulilo River, at Butembo–Beni road	29.32523	00.18327	0.5–1
3	North-Kivu	Tandibo River, at road bridge	29.74522	00.32023	0.5
4	North-Kivu	Semliki River / Lake Edward	29.60163	-00.13958	0.5
5	North-Kivu	Lake Edward	29.56668	-00.15330	3–5
6	North-Kivu	Lake Edward	29.55108	-00.15642	3–5
7	North-Kivu	Lake Edward close to inlet of Muko River	29.52738	-00.16377	3–5
8	North-Kivu	Lake Edward	29.52025	-00.16340	3–5
9	North-Kivu	Lake Edward close to inlet of Tchumbwe River	29.49640	-00.17288	3–5
10	North-Kivu	Lake Edward	29.48502	-00.18582	3–5
11	North-Kivu	Semliki River	29.57148	-00.11697	2–3
12	North-Kivu	Semliki River	29.56837	-00.12527	2–3
13	North-Kivu	Semliki River	29.58710	-00.13943	2–3
14	Orientale	Liango Creek, river bend at road bridge	29.69279	01.23876	0.2
15	Orientale	Loya River at bridge on Beni–Mambasa road	29.69570	01.26568	0.5
16	Orientale	River at bridge on Komanda–Mambasa road	29.49175	01.34806	0.5
17	Orientale	River at bridge on Komanda–Mambasa road	29.27945	01.36966	0.2
18	Orientale	Buluduma Creek at small wooden bridge	29.03787	01.36414	0.1
19	Orientale	Binase River at crossroads	29.03429	01.35492	0.3
20	Orientale	Irrigation channel at Binase River	29.03429	01.35492	0.1
21	Orientale	Mangodoku Creek at small wooden bridge	29.02856	01.34828	0.1
22	Orientale	Kangambili River at wooden bridge	29.02604	01.34870	0.2
23	Orientale	Pemba River at bridge at Mambasa–Nia-Nia road	28.99355	01.37608	0.1–0.3
24	Orientale	Abunagwa River at a bridge at Mambasa–Nia-Nia road	28.98827	01.37169	0.1

TABLE 2

Collection sites with their respective sampled species. Collection sites are separated into sites of the Nile and the Congo drainage system. Note that localities 1 and 2 are part of the Congo system. Coding: x – alive specimens, s – shells only. Lacustrine habitats (Lake Edward) are highlighted in grey.

	Nile drainage system										Congo drainage system														
	3	4	5	6	7	8	9	10	11	12	13	1	2	14	15	16	17	18	19	20	21	22	23	24	
Gastropoda																									
<i>P. ovata</i>																		x							
<i>G. humerosa</i>			x	x		x		x	x	x										x				x	
<i>P. ignobilis</i>												x													
<i>P. liricincta</i>														x											
<i>M. tuberculata</i>		x	x	x	x	x	x	x	x	x	x					x	x	x				x			
<i>L. natalensis</i>												x						x							
<i>B. pfeifferi</i>												x													
<i>B. smithi</i>										x	x														
<i>B. cf. stanleyi</i>										x															
<i>B. cf. forskalii</i>																						x			
<i>B. cf. truncatus</i>																						x			
<i>C. kigeziensis</i>										s	x	s													
<i>Gyraulus</i> sp.												x													
Bivalvia																									
<i>C. stuhlmanni</i>				x			x		x	x	x														
<i>M. dubia</i>		x																							
<i>C. fluminalis</i>			x	x		x		x	x	x	x														
<i>S. hartmanni</i>																								x	
<i>P. cf. casertanum</i>	x																								
<i>P. kenianum</i>													x												
<i>P. pirothi</i>																									
Total	1	2	3	4	4	1	5	1	6	7	8	3	2	1	1	1	1	1	2	1	2	1	3	2	1

Family Bithyniidae Gray, 1857
Gabbiella humerosa (Martens, 1879)
G. h. edwardi (Mandahl-Barth, 1954)

Fig. 2E

Bithynia stanleyi var. *humerosa*: Martens 1879: 104. (Type locality: “aus dem Victoria Nianza (Ukerewe), an dessen Südweststrand”)

Gabbia (*Parabithynia*) *humerosa edwardi*: Mandahl-Barth 1954: 55, figs 23c–d. (Type locality: “Northern part of Lake Edward, immediately east of the border of the Congo, in shallow water”)

Taxonomic remarks: Mandahl-Barth (1968) recognised four other subspecies (*alberti*, *kivuensis*, *kyogae*, and *tanganyicensis*), each one reported from the eponymous lake, as well as a fifth, *G. h. humerosa*, from L. Victoria. The subspecies from L. Edward is reported to be the largest of these taxa.

Habitat description: We found this species in vast abundance in L. Edward (at depths of 3–5 m) as well as in the Semliki R. (at depths of 2–3 m).

Collecting sites: 5, 6, 8, 10, 11, 12, 13.

IUCN Red List Category: Least Concern (Jørgensen 2008a).

Family Pachychilidae P. Fischer & Crosse, 1892
Potadoma ignobilis (Thiele, 1911)

Fig. 2B

Melania ignobilis: Thiele 1911: 211, pl. 5, fig. 53. (Type locality: “Im Ituri bei Mawambi”)

Taxonomic remarks: The species *Potadoma mungwana* Pilsbry & Bequaert, 1927 was synonymized with *P. ignobilis* by Mandahl-Barth (1967). The genus has a disjunctive distribution with *P. ignobilis* and *P. liricincta*, being dominant in the Eastern Congo (see Brown 1994: 149).

Habitat description: We found this species in moderate abundance at a depth of 0.2 m in the Liango Creek on sandy substrate (Figs 4E, 4F).

Collecting site: 14.

IUCN Red List Category: Least Concern (Jørgensen 2008b).

Potadoma liricincta (Smith, 1888)

Fig. 2C

Melania liricincta: Smith 1888: 52, fig. 1. (Type locality: “Albert Nyanza, probably from the eastern side of the Lake”)

Taxonomic remarks: Mandahl-Barth (1967) synonymized the following four species from the Congo under *P. liricincta*: *Melania tornata* Martens, 1897; *P. pokoensis*, Pilsbry & Bequaert, 1927; *P. medjeorum* Pilsbry & Bequaert, 1927; *P. urundica* Thiele, 1911. The type locality is probably wrong since *Potadoma* has not been reported since from L. Albert (e.g., Brown 1994; Mandahl-Barth 1967; RS pers. observ.).

Habitat description: We have found this species in flowing waters at collecting depths of 0.2–0.5 m on varying substrates (gravel and sand with proportions of clay and detritus; Figs 4G–I).

Collecting sites: 15, 16, 17, 19, 22, 23.

IUCN Red List Category: Near Threatened (Jørgensen 2008c).

Family Thiaridae Gill, 1871
Melanoides tuberculata (O.F. Müller, 1774)

Fig. 2D

Nerita tuberculata: O.F. Müller 1774: 191. (Type locality: “In littore Coromandel”, India)

Taxonomic remarks: *M. tuberculata* is probably an aggregation of several species (e.g., Genner *et al.* 2007*b* and references therein). As a taxonomic revision is beyond the scope of this paper, we here follow Mandahl-Barth (1954) and Brown (1994). Falkner (1991) suggested the correct species name to be *tuberculatus* due to the masculine gender of the genus name. Yet, the author of the genus (Oliver 1804) treated the gender as feminine (*ibid.*: 40) and hence the correct name is *tuberculata* (according to ICZN 30.1.4.4.).

Habitat description: We found this species in great abundance at every sampled locality at L. Edward as well as in the Semliki R.

Collecting sites: 4, 5, 6, 7, 8, 9, 10, 11, 12, 13.

IUCN Red List Category: Least Concern (Madhyastha 2010).

Family Lymnaeidae Rafinesque, 1815
Limnaea (Radix) natalensis Krauss, 1848

Fig. 2H

Limnaeus natalensis: Krauss 1848: 85, pl. 5, fig. 15. (Type locality: “In stagnis natalensibus”, South Africa)

Taxonomic remarks: Hubendick (1951) synonymized all hitherto described species in Africa under *L. natalensis*. Recent molecular phylogenetic studies have indicated that *L. natalensis* belongs to the genus or subgenus *Radix* (Albrecht *et al.* 2008; Correa *et al.* 2010). In the absence of a thorough generic revision of the Lymnaeidae, we tentatively refer here to *L. (Radix) natalensis*.

Habitat description: The species was found in a small, slowly flowing creek next to a cornfield (18; Fig. 4H) and within irrigation channels (1, 20). The substrate comprised clay, sapropel and detritus.

Collecting sites: 1, 18, 20.

IUCN Red List Category: Least Concern (Appleton *et al.* 2009*c*).

Family Planorbidae Rafinesque, 1815
Biomphalaria cf. pfeifferi (Krauss, 1848)

Fig. 2L

Planorbis pfeifferi: Krauss 1848: 83, pl. 5, fig. 7. (Type locality: “In Umgani [= Umgeni]-Valley, Natal”)

Taxonomic remarks: Based on molecular genetics, Jørgensen *et al.* (2007*b*) suggested *pfeifferi* to be paraphyletic. Since a revision of this taxon based on DNA data is still pending, we identify our specimens tentatively.

Habitat description: We collected the species from irrigation channels watering fields near the Mususa R. south of Butembo. The substrate comprised mainly clay and sapropel.

Collecting site: 1.

IUCN Red List Category: Not Evaluated (*B. pfeifferi*).

Biomphalaria smithi Preston, 1910

Fig. 2M

Biomphalaria smithi: Preston 1910: 535, figs 26, 26A. (Type locality: "Lake Albert Edward")

Taxonomic remarks: A unique, distinct character of this species is the sharp slope of the last whorl. Mandahl-Barth (1957a) notes however that this feature may not be developed in immature specimens. The species is endemic to L. Edward and its immediate surroundings (Mandahl-Barth 1957a; Brown 1994; Jørgensen *et al.* 2007b).

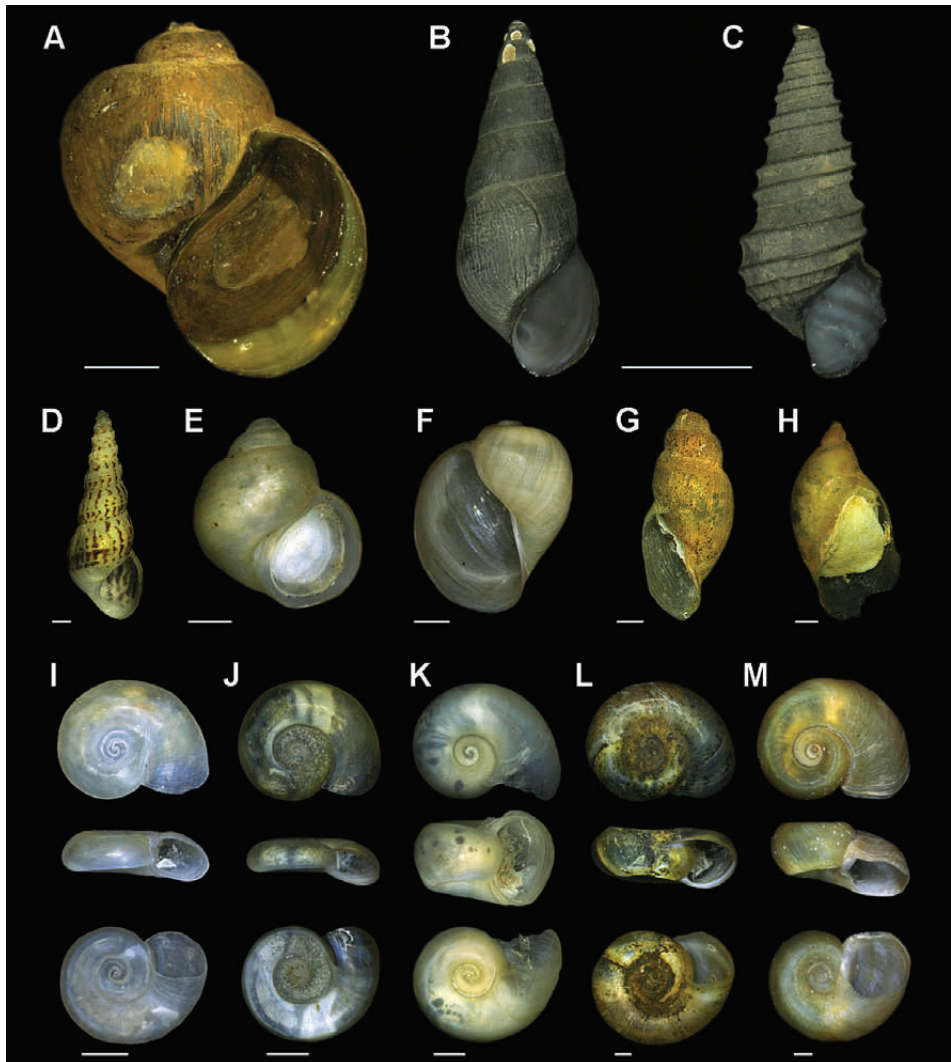


Fig. 2. Gastropod species collected in the Eastern Congo: (A) *Pila ovata*; (B) *Potadoma ignobilis*; (C) *Potadoma liricincta*; (D) *Melanoides tuberculata*; (E) *Gabbiella humerosa*; (F) *Bulinus* cf. *truncatus*; (G) *Bulinus* cf. *forskalii*; (H) *Lymnaea (Radix) natalensis*; (I) *Ceratophallus kigeziensis*; (J) *Gyraulus* sp.; (K) *Biomphalaria* cf. *stanleyi*; (L) *Biomphalaria* cf. *pfeifferi*; (M) *Biomphalaria smithi*. Scale bars: 10 mm for A–C and 1 mm for D–M.

Habitat description: The species was dredged from L. Edward (formerly named Lake Albert Edward; see type locality) as well as from the Semliki R. at depths of 2–5 m on sandy substrates.

Collecting sites: 10, 11, 12.

IUCN Red List Category: Near Threatened (Kyambadde 2004).

Biomphalaria cf. stanleyi (Smith, 1888)

Fig. 2K

Planorbis stanleyi: Smith 1888: 55. (Type locality: “Albert Nyanza, probably from the eastern side of the Lake”)

Taxonomic remarks: This species was (in addition to its type locality) reported from L. Chad (Brown 1974) and L. Cohoha (Gryseels *et al.* 1987) but not from L. Edward or the upper Semliki. Since our specimens are immature, we identify them tentatively.

Habitat description: We dredged this species from the Semliki R. at depths of 2–3 m together with (amongst others) *B. smithi*. The sampled specimens are apparently immature yet differ considerably from also sampled immature specimens of *B. smithi*.

Collecting site: 11.

IUCN Red List Category: Data Deficient (*B. stanleyi*) (Lange 2004).

Bulinus cf. forskalii (Ehrenberg, 1831)

Fig. 2G

Isidora forskalii: Ehrenberg 1831: 20, pl. 20. (Type locality: Damietta, Egypt)

Taxonomic remarks: The shell morphology and dimensions of this species vary considerably, which led to a large number of named species (see Mandahl-Barth 1957*b* for a list of synonyms). The species is similar to *B. scalaris*, which in turn is morphologically similar to *B. canescens*. All three species have the same chromosome number ($2n = 36$; Brown 1994).

Habitat description: We found this species in the slowly flowing creek Mangodoku (Fig. 4J) as well as in the Kangambili R., both in the vicinity of Mambasa village. The substrate was dominated by clay and detritus. This may be a new report for this species, which is currently not mentioned in the IUCN list for this area.

Collecting sites: 21, 22.

IUCN Red List Category: Least Concern (*B. forskalii*) (Appleton *et al.* 2009*b*).

Bulinus cf. truncatus (Audouin, 1827)

Fig. 2F

Physa truncatus: Audouin 1827: 166, fig. 27. (Type locality: Egypt)

Taxonomic remarks: This morphologically variable species is the only tetraploid taxon of the genus (save *B. permembranaceus*; Brown 1994). In the absence of chromosomal information we tentatively designate the sampled specimens to this species. Mandahl-Barth (1957*b*) mentions a subspecies *trigonus*, which occurs in lakes Victoria and Edward.

Habitat description: We dredged this species in L. Edward and in the Semliki R. on sandy substrate at depths of 3–5 and 2–3 m respectively. Note that the former sample consists of empty shells only.

Collecting sites: 8, 12.

IUCN Red List Category: Not Evaluated (*B. truncatus*).

Ceratophallus kigeziensis (Preston, 1912)

Fig. 2I

Planorbis kigeziensis: Preston 1912: 190, pl. 32, figs 5a, b. (Type locality: “Kigezi, extreme S.W. Uganda, at an altitude of 6000 ft.”)

Planorbis (Gyraulus) avakubiensis: Pilsbry & Bequaert 1927: 127, fig. 9. (Type locality: “Avakubi, in a woodland pool”)

Taxonomic remarks: Mandahl-Barth (1954) reports several localities for this species from Uganda, but also mentioned its possible occurrence in Rwanda and Burundi. Brown (1994) suggested that *avakubiensis* might be conspecific with *kigeziensis*. The former taxon was described by Pilsbry and Bequaert (1927) from near Nia-Nia, approximately 200 km west of our locality 24.

Habitat description: This species was dredged from L. Edward and the Semliki R. Note that the samples from localities 10 and 12 consist of empty shells only.

Collecting sites: 10, 11, 12.

IUCN Red List Category: Least Concern (Jørgensen & Van Damme 2009).

Gyraulus sp.

Fig. 2J

Taxonomic remarks: It is not possible to determine the species of our single specimen. Based on the position of the kidney and the absence of a sclerotized penis, we can however exclude that the specimen belongs to the genus *Ceratophallus*. According to Brown (1994) *G. costulatus* is the only widespread *Gyraulus* species in Africa and it was reported from L. Edward by Mandahl-Barth (1954). Yet our specimen from the Semliki R. does not possess strong ribs and a carina.

Habitat description: The species was dredged in the Semliki R. at depths of 2–3 m from sandy substrate.

Collecting site: 12.

Bivalvia

Family Unionidae Rafinesque, 1820

Coelatura stuhlmanni (Martens, 1897)

Figs 3B, 3C

Unio stuhlmanni: Martens 1897: 231, pl. 7, fig. 13. (Type locality: “Albert-Edward-See bei Vitschumbi”)

Taxonomic remarks: Mandahl-Barth (1988) regarded *stuhlmanni* as well as its supposed sister taxon *bakeri* as subspecies of *aegyptica*. However, Scholz and Glaubrecht (2004), in concordance with Daget (1998), argued for a species status for both taxa and we follow their view here. Graf and Cummings (2007) suggested that *C. bakeri* and *C. stuhlmanni* may not be endemic to L. Albert and L. Edward respectively, but occur in both lakes.

Habitat description: We found this species in moderate abundance at depths of 3–5 m at the north-western shore of L. Edward (Fig. 4C) and in the Semliki R. (Fig. 4D). In the river, Mandahl-Barth (1954) anticipated a “shorter form ... with less marked zig-zag sculpture ... forming a transitional link between *C. stuhlmanni* and *C. bakeri*” (ibid.: 129). We compared eight specimens collected from three localities in L. Edward with 11 specimens from two localities in the Semliki. Whereas the zigzag sculpture is indeed partly less marked in the Semliki R., the riverine specimens are not shorter than the lake form (Fig. 3B, riverine form; Fig. 3C, lake form).

Collecting sites: 6, 8, 10, 11, 12.

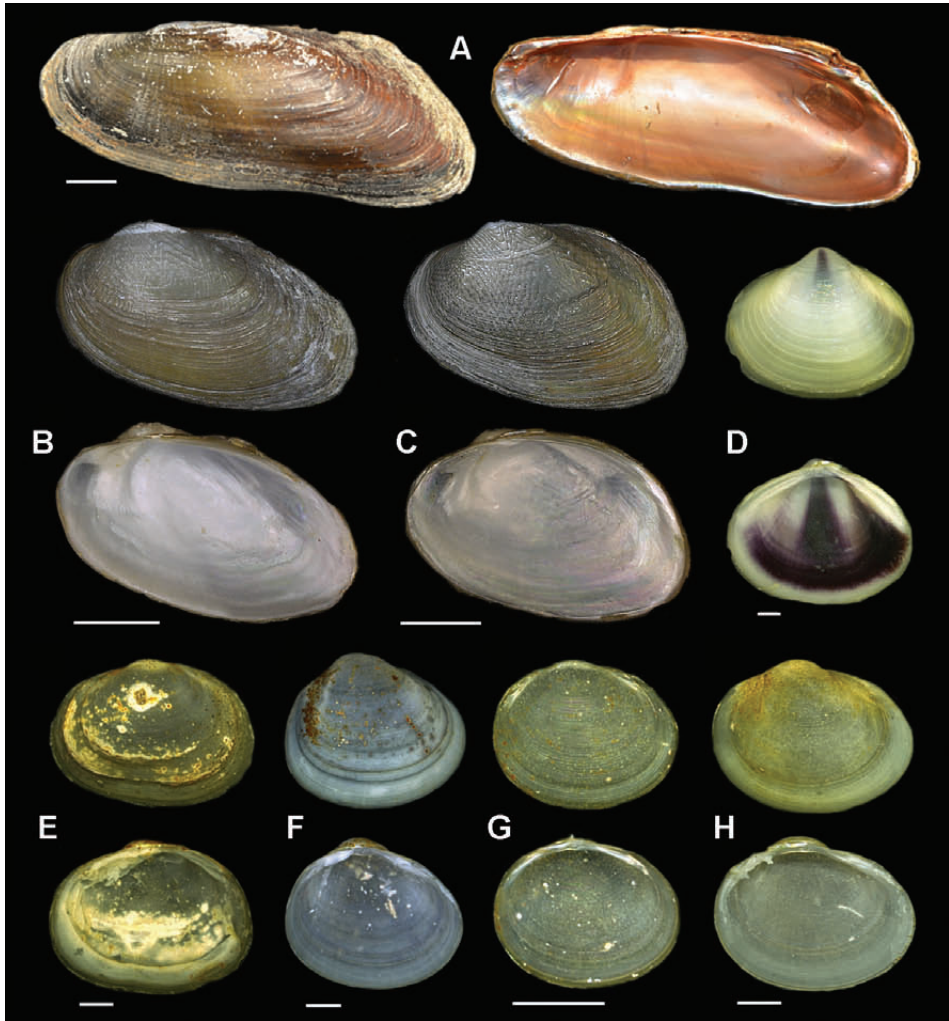


Fig. 3. Bivalve species collected in the Eastern Congo: (A) *Mutela dubia*; (B) *Coelatura stuhlmanni* from the Semliki River; (C) *Coelatura stuhlmanni* from Lake Edward; (D) *Corbicula fluminalis*; (E) *Sphaerium hartmanni*; (F) *Pisidium kenianum*; (G) *Pisidium pirothi*; (H) *Pisidium* cf. *casertanum*. Scale bars: 10 mm for A–C and 1 mm for D–H.

IUCN Red List Category: Not Evaluated.

Family Iridinidae Swainson, 1840
Mutela dubia (Gmelin, 1791)

Fig. 3A

Mutela dubia: Adanson 1757: 234, pl. 17, fig. 21. (Pre-Linnaean; type locality: “dans les lacs d’eau douce”, Senegal)

Mytilus dubius: Gmelin 1791: 3363. (Type locality: as given by Adanson 1757)

Taxonomic remarks: To our knowledge this species has not been reported from L. Edward in the literature, but specimens from that locality are deposited in various museum collections (e.g., Academy of Natural Sciences of Philadelphia, No. 164951; Museum of Comparative Zoology, Harvard University, Nos 172816 & 171875; see <http://mussel-project.ua.edu>, accessed 10 September 2011). Mandahl-Barth (1988) divided the species into four geographical subspecies of which our specimens resembles *M. d. emini* (Martens, 1897). However, this subspecies is reported to be endemic to L. Albert (Mandahl-Barth 1988).

Habitat description: The specimens were collected at the intersection of L. Edward and the Semliki R. by local fishermen close to our original locality 4.

Collecting site: 4.

IUCN Red List Category: Least Concern (Graf *et al.* 2009).

Family Corbiculidae Gray, 1847
Corbicula fluminalis (O.F. Müller, 1774)
C. f. cunningtoni Smith, 1906

Fig. 3D

Tellina fluminalis: O.F. Müller 1774: 205. (Type locality: “In fluvio Asiae Euphrat.”)

Corbicula cunningtoni: Smith 1906: 186, pl. 10, fig. 15. (Type locality: Lake Victoria “at Bukoba on the west shore of the Lake.”)

Corbicula radiata edwardi: Pilsbry & Bequaert 1927: 343, figs 73a, b. (Type locality: “Lake Edward at Kabare”)

Taxonomic remarks: Whereas the form from L. Edward was originally treated as subspecies of *radiata* (Pilsbry & Bequaert 1927), Mandahl-Barth (1988) synonymized all African *Corbicula* under the name *fluminalis* with the exception of *C. astartina*. The author suggested that the originally described subspecies from L. Edward (*C. radiata edwardi*) is not very different from the subspecies *cunningtoni* and hence the former name “perhaps ought not to be maintained” (ibid.: 115). More recent taxonomic accounts agree with this classification (Daget 1998; Korniusshin 2004). As to whether all African *Corbicula* are indeed *fluminalis* is unclear as the question still awaits a molecular based systematic revision (see Pfenninger *et al.* 2002).

Habitat description: We found this species in moderate abundance at depths of 3–5 m at the north-western shore of L. Edward as well as at depths of 2–3 m in the Semliki R. on predominantly sandy substrate.

Collecting sites: 5, 6, 8, 10, 11, 12, 13.

IUCN Red List Category: Not Evaluated.

Family Sphaeriidae Deshayes, 1855
Sphaerium hartmanni (Jickeli, 1874)

Fig. 3E

Cyclas hartmanni: Jickeli 1874: 292, pl. 11, fig. 15. (Type locality: “aus Nubien”)

Taxonomic remarks: Mandahl-Barth (1988) synonymized a number of former species under this name and ranked them as subspecies. Based on nephridia characteristics, Korniusshin (1998) suggested that all African *Sphaerium* spp. should be transferred to the genus *Musculium*. In the absence of a molecular phylogenetic analysis of African material and the general confusion of *Musculium* versus *Sphaerium* (see Lee & Ó Foighil 2003), we here retain the generic affiliation most commonly used.

Habitat description: We collected this species from the Pemba R. at the road from Mambasa to Nia-Nia from a depth of 0.1–0.3 m. The substrate comprised sand and gravel.

Collecting site: 23.

IUCN Red List Category: Least Concern (Ghamizi *et al.* 2009b).

Pisidium cf. casertanum (Poli, 1791)

Fig. 3H

Cardium casertanum: Poli 1791: 65, pl. 16, fig. 1. (Type locality: “in rivuli Alveo per regium Casertae”, Italy)

Taxonomic remarks: This species is reported to be cosmopolitan (e.g., Kuiper 1966; Mandahl-Barth 1988), but recent molecular studies indicate that this taxon is not monophyletic and comprises several species (Lee & Ó Foighil 2003; Schultheiß *et al.* 2008). Thus, we identify it tentatively. Although the shell shape is similar to *P. viridarium*, our specimens are missing a callus—a typical hinge character of *P. viridarium*. Moreover, preliminary molecular analyses indicate that the specimens described here do not cluster with specimens of *P. viridarium* from its type locality (unpubl. data).

Habitat description: We found this species near Mutwanga town in the Tandibo R. at the foot of the Rwenzori Mountains. The substrate consisted mainly of sand and gravel.

Collecting site: 3.

IUCN Red List Category: Least Concern (*P. casertanum*) (Budha 2010).

Pisidium kenianum Preston, 1911

Fig. 3F

Pisidium kenianum: Preston 1911: 475, fig. 36. (Type locality: “Between Rumruti and Mount Kenia”)

Taxonomic remarks: The Congo material was compared to recently collected specimens from the type locality, which strongly supports our designation. Note, however, that the status of this species is somewhat disputed (Mandahl-Barth 1988). A phylogenetic analysis based on morphological characters placed the species near *P. casertanum* and *P. compressum* (Korniusshin & Glaubrecht 2006). In the Congo it is known from Katanga Prov. (former Shaba region; Daget 1998).

Habitat description: We collected this species from the Luulilo R. near Butembo town at depths of 0.5–1 m (Fig. 4F). The substrate comprised stones and gravel with minor proportions of sand and clay.

Collecting site: 2.

IUCN Red List Category: Data Deficient (Lange & Van Damme 2009).

Pisidium pirothi Jickeli, 1881

Fig. 3G

Pisidium pirothi: Jickeli 1881: 340. (Type locality: "Harasa zwischen Atbara und Bassalam", Sudan)

Taxonomic remarks: This species is known to be widely distributed in Africa. However, a large variability in shell characteristics is evident in this taxon, as in many of the other African species of the genus (Albrecht *et al.* 2010). Thus a comprehensive phylogenetic and taxonomic treatment of African Sphaeriidae is overdue.

Habitat description: The species was sampled from the Kangambili R. in the vicinity of Mambasa town at a depth of 0.2 m. The substrate comprised mainly clay and detritus.

Collecting site: 22.

IUCN Red List Category: Least Concern (Appleton *et al.* 2009a).

RESULTS AND DISCUSSION

Taxa from the Nile drainage system

We investigated localities from two separate areas of the Nile drainage system in the North-Kivu Province: (1) Lake Edward and the Semliki River, and (2) the western hillsides of the Rwenzori Mountains (Figs 1, 4B–D). The latter area was investigated at the foot of the mountains as well as up to an altitude of 2138 m (i.e. near Kalonge hut on the Congolese Rwenzori Mountains trail). Despite intensive search in creeks and rivers on the way to the hut, neither live molluscs nor shells were found. Indeed, apart from leeches we did not find freshwater invertebrates at all. At the foot of the mountains near Mutwanga town, we collected specimens of *Pisidium* cf. *casertanum* (Fig. 3H).

Compared to the investigated riverine habitats, Lake Edward was species rich. We found a subset of eight molluscan species (Mandahl-Barth 1954, 1988; Brown 1994; Table 2), including two out of four proposed endemic taxa: *Gabbiella humerosa edwardi* and *Biomphalaria smithi* (see "Biodiversity and conservation" section). Additionally, we sampled the Semliki River approximately 6 km downstream but were discouraged by rangers from continuing due to poaching activity in the area (Figs 4C, 4D). In total, we found seven gastropod and four bivalve species in the Nile drainage system.

Taxa from the Congo drainage system

We investigated freshwater habitats along the road from Beni to Mambasa via Komanda. Between the latter two towns the road passes through the Ituri forest and frequently crosses rivers and creeks (Figs 1, 4E–G). On the way to Mambasa we found only *Potadoma* in these waters (localities 14–17 in Fig. 1; Figs 2B, 2C). This scarcity of molluscs in the Ituri region has already been mentioned by Brown (1994: 539). Our sampling efforts were severely hampered by the dense forest, which allowed only limited exploration of the creeks and rivers (Fig. 4G). Within and in the vicinity of Mambasa, we additionally found *Pila ovata* as well as *Bulinus* cf. *forskali* and *Lymnaea* (*Radix*) *natalensis* (Figs 2A, 2G, 2H). The latter two species are known as intermediate hosts



Fig. 4. Selected localities: (A) Luulilo R. near Butembo (locality 2); (B) creek in the Rwenzori Mountains near Kalonge Hut (image courtesy of F. Bauer); (C) north-western shore of L. Edward; (D) view from Ishango at the outflow of the Semliki R.; (E) Liango Creek at the road from Beni to Komanda (14); (F) same locality with *Potadoma ignobilis* visible on the sandy substrate; (G) Loya R. in the Ituri forest at the bridge on the road from Komanda to Mambasa (15); (H) Buluduma Creek next to a cornfield in Mambasa (18); (I) Binase R. (19); (J) Mangodoku Creek in Mambasa (21).

of the parasites *Schistosoma* and *Fasciola*, respectively (Brown 1994). Additionally, we collected *Biomphalaria* cf. *pfeifferi* and *L. (Radix) natalensis* from the Mususa River as well as *Pisidium kenianum* in the vicinity of Butembo (localities 1 and 2 in Fig. 1; Table 2). In total, we found six gastropod and three bivalve species in the Congo drainage system.

Biodiversity and conservation

The on-site molluscan species diversity in the investigated area ranged from one to eight species, with the highest diversity in the Semliki R. and in L. Edward (Table 2). Of the sampled species, two are assessed as Data Deficient and 11 as Least Concern in the IUCN Red List of endangered species. Two species, *Biomphalaria smithi* and *Potadoma liricincta* fulfil the criteria for being Near Threatened (Kyambadde 2004; Jørgensen 2008c). *P. liricincta* was reported from two localities in the Ituri rainforest (Jørgensen 2008c). We found this species in six different creeks and rivers in the Ituri region (Table 2).

Biomphalaria smithi was not known from the Congolese side of L. Edward (Kyambadde 2004) yet we found the species there, as well as in the Semliki R. Acknowledging that we surveyed only a confined part of L. Edward, it is noteworthy that two potentially endemic taxa, *Burnupia edwardi* and *Ceratophallus apertus*, were not found and we collected only approximately half of the species reported from the lake during our study (Mandahl-Barth 1954, Brown 1994). Further mollusc surveys on both sides of the lake are necessary in order to estimate the faunal change during the past decades. This becomes even more important in light of ongoing eutrophication, pollution and boat traffic (Kyambadde 2004), as well as oil exploration activities in the lake and its basin.

Taxonomic uncertainty and concluding remarks

In the past decade, phylogenetic investigations of African freshwater molluscs have frequently called former taxonomic assignments into question (e.g., Genner *et al.* 2007b; Jørgensen *et al.* 2007a, b; Schultheiß *et al.* 2009, 2011; Sengupta *et al.* 2009). The incongruence between morphological and molecular data often has two immediate consequences. First, it leads to taxonomic instability and second, it changes the number of species known for the investigated area, which constitutes essential information for conservation efforts. Against this background, the assignment and distribution of freshwater mollusc species must be treated with some caution as long as molecular revisions are absent.

An interesting outcome of our pilot study is the clear faunal break between species of the two great river systems. We are aware, however, that our survey is rather limited and thus the observed break may partly be a sampling artefact. Finally, we would like to stress the importance of further faunal studies in order to allow more informed decisions on the conservation status, taxonomic assignments, phylogenetic relationships and biogeographic origins of the mollusc fauna of the Eastern Congo region.

ACKNOWLEDGEMENTS

Vikandy S. Mambo (Ruwenzori State University) is gratefully acknowledged for technical support during the fieldwork and Friederike Bauer (University Heidelberg) for logistic help in the Rwenzori Mountains. We thank Aslak Jørgensen for kindly sharing his knowledge on planorbis species and Daniel L. Graf for helpful remarks on the *Coelatura* specimens from Lake Edward and the Semliki River. We thank Eike Neubert (Natural History Museum Bern) for crucial information regarding an original description. Thomas Wilke and Sergej Sereda commented on an earlier version of the manuscript, and Torsten Hauffe helped with the GIS. In particular we would like to thank Dirk Van Damme for his constructive and insightful review. This study was funded by the DFG projects SCHR352/9-1 and AL1076/6-2.

REFERENCES

- ABELL, R., THIEME, M.L., REVENGA, C., BRYER, M., KOTTELAT, M., BOGUTSKAYA, N., COAD, B., MANDRAK, N., BALDERAS, S.C., BUSSING, W., STIASSNY, M.L.J., SKELTON, P., ALLEN, G.R., UNMACK, P., NASEKA, A., NG, R., SINDORF, N., ROBERTSON, J., ARMUO, E., HIGGINS, J.V., HEIBEL, T.J., WIKRAMANAYAKE, E., OLSON, D., LÓPEZ, H.L., REIS, R.E., LUNDBERG, J.G., SABAJ PÉREZ, M.H. & PETRY, P. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* **58**: 403–414.
- ADANSON, M. 1757. *Histoire naturelle du Sénégal*. Coquillages. Avec la relation abrégée d'un voyage fait en ce pays pendant les années 1749, 50, 51, 52 & 53. Ouvrage orné de figures. Paris: Bauche.
- ALBRECHT, C., WOLFF, C., GLÖER, P. & WILKE, T. 2008. Concurrent evolution of ancient sister lakes and sister species: the freshwater gastropod genus *Radix* in lakes Ohrid and Prespa. *Hydrobiologia* **615**: 157–167.
- ALBRECHT, C., BÖSSNECK, U., GEERTZ, T., WESTERMANN, M., LANGE, C. & SCHULTHEISS, R. 2010. Exploring the unexplored: the high-mountain endemic pea-clam (*Bivalvia*: Sphaeriidae: *Pisidium* spp.) fauna of East Africa. *Tropical Natural History* **Suppl. 3**: 242.
- APPLETON, C. 1979. The Unionacea (Mollusca, Lamellibranchiata) of South-Central Africa. *Annals of the South African Museum* **77**: 151–174.
- APPLETON, C., GHAMIZI, M., JØRGENSEN, A., KRISTENSEN, T.K., LANGE, C.N., STENSGAARD, A.-S. & VAN DAMME, D. 2009a. *Pisidium pirothi*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- APPLETON, C., GHAMIZI, M., JØRGENSEN, A., KRISTENSEN, T.K., NGEREZA, C., STENSGAARD, A.-S. & VAN DAMME, D. 2009b. *Bulinus forskalii*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- APPLETON, C., GHAMIZI, M., JØRGENSEN, A., KRISTENSEN, T.K., STENSGAARD, A.-S. & VAN DAMME, D. 2009c. *Lymnaea natalensis*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- AUDOUIN, V. 1827. Explication sommaire des planches de Mollusques de l'Égypte et de la Syrie. In: Savigny, J.-C., ed., *Description de l'Égypte ou Recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française*. Paris: C.L.F. Panckoucke, pp. 117–212.
- BALUKU, B., JOSENS, G. & LOREAU, M. 1989. Etude préliminaire de la densité et de la répartition des mollusques dans deux cours d'eau du Zaïre oriental. *Revue de Zoologie Africaine* **103**: 291–302.
- BENGTSON, P. 1988. Open nomenclature. *Palaentology* **31**: 223–227.
- BOUCHET, P. & ROCROI, J.P. 2005. Classification and nomenclator of gastropod families. *Malacologia* **47**: 1–397.
- BOUCHET, P., ROCROI, J.P., BIELER, R., CARTER, J.G. & COAN, E.V. 2010. Nomenclator of bivalve families with a classification of bivalve families. *Malacologia* **52**: 1–184.
- BROWN, D.S. 1974. A survey of the Mollusca of Lake Chad, Central Africa. Appendix A. Report on a collection of Planorbidae and Ancyliidae. *Revue de Zoologie Africaine* **88**: 331–343.
- 1994. *Freshwater snails of Africa and their medical importance*. London: Taylor & Francis.
- BUDHA, P.B. 2010. *Pisidium casertanum*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- CHARTIER, C., BUSHU, M., NGENDAHAYO, L.D. & BAYSSADE-DUFOUR, C. 1990a. *Bulinus africanus* from Ituri (North-East Zaïre) as a host for *Schistosoma bovis*. *Annales de la Société belge de Médecine tropicale* **70**: 159–161.
- CHARTIER, C., NGOTA, A., LONU, L. & CABARET, J. 1990b. Dynamics of *Lymnaea natalensis* populations in the Bunia area (Ituri, Haut-Zaïre). *Annales de Parasitologie Humaine et Comparée* **65**: 177–182.
- CHARTIER, C., BUSHU, M., KRISTENSEN, T.K., NZEYMANA, S., LUBINGO, M. & CABARET, J. 1992. Inventaire des mollusques d'eau douce en Ituri (Haut-Zaïre). Conséquences sanitaires pour l'homme et le bétail. *Revue d'hydrobiologie tropicale* **25**: 189–196.
- CHARTIER, C., CABARET, J., BUSHU, M. & KRISTENSEN, T.K. 1993. Environmental and geographical distribution in north-east Zaïre of intermediate hosts of bovine fascioliasis (*Lymnaea natalensis*) and schistosomiasis (*Bulinus africanus*). *Journal of Molluscan Studies* **59**: 117–119.
- CORREA, C.A., ESCOBAR, J.S., DURAND, P., RENAUD, F., DAVID, P., JARNE, P., POINTIER, J.-P. & HURTREZ-BOUSSÉS, S. 2010. Bridging gaps in the molecular phylogeny of the Lymnaeidae (Gastropoda: Pulmonata), vectors of Fascioliasis. *BMC Evolutionary Biology* **10**: 381.
- DAGET, J. 1998. *Catalogue raisonné des Mollusques bivalves d'eau douce africains*. Orstom, Leiden, Paris: Backhuys Publishers.
- EHRENBERG, C.G. 1831. Animalia Mollusca. In: Hemprich, F.G. & Ehrenberg, C.G., eds, *Symbolae Physicae, sive icones et descriptiones corporum naturalium novorum aut minus cognitorum, que ex itineribus per Libyam, Aegyptum, Nubiam, Dongolam, Syriam, Arabiam et Habessiniam; 1. Pars Zoologica. Animalia Evertebrata*. Berlin, pp. 1–46.

- FALKNER, G. 1991. Vorschlag für eine Neufassung der Roten Liste der in Bayern vorkommenden Mollusken (Weichtiere), mit einem revidierten systematischen Verzeichnis der in Bayern nachgewiesenen Molluskenarten. *Schriftenreihe des Bayerischen Landesamtes für Umweltschutz* **97**: 61–112.
- FRANSEN, F., BENNIKE, T. & CRIDLAND, C.C. 1978. Studies on *Schistosoma intercalatum* Fisher, 1934 and its intermediate snail host in the Kisangani area, Zaire. *Annales de la Société belge de Médecine tropicale* **58**: 21–31.
- GENNER, M.J., NICHOLS, P., CARVALHO, G., ROBINSON, R.L., SHAW, P.W., SMITH, A. & TURNER, G.F. 2007a. Evolution of a cichlid fish in a Lake Malawi satellite lake. *Proceedings of the Royal Society Series B – Biological Sciences* **274**: 2249–2257.
- GENNER, M.J., TODD, J.A., MICHEL, E., ERPENBECK, D., JIMOH, A., JOYCE, D.A., PIECHOCKI, A. & POINTIER, J.P. 2007b. Amassing diversity in an ancient lake: evolution of a morphologically diverse parthenogenetic gastropod assemblage in Lake Malawi. *Molecular Ecology* **16**: 517–530.
- GHAMIZI, M., JØRGENSEN, A., KRISTENSEN, T.K., LANGE, C., STENSGAARD, A.-S. & VAN DAMME, D. 2009a. *Pila ovata*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- GHAMIZI, M., KRISTENSEN, T.K., STENSGAARD, A.-S. & VAN DAMME, D. 2009b. *Musculium hartmanni*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- GLAUBRECHT, M. 2008. Adaptive radiation of thalassoid gastropods in Lake Tanganyika, East Africa: morphology and systematization of a paludomid species flock in an ancient lake. *Zoosystematics and Evolution* **84**: 71–122.
- GLAUBRECHT, M. & STRONG, E.E. 2007. Ancestry to an endemic radiation in Lake Tanganyika? Evolution of the viviparous gastropod *Potadomoides* Leloup, 1953 in the Congo River system (Caenogastropoda, Cerithioidea, Paludomidae). *Biological Journal of the Linnean Society* **92**: 367–401.
- GMELIN, J.F. 1791. In: Linné, C., v. , ed., *Systema naturae per regna tria naturae : secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Lipsiae: Impensis Georg. Emanuel. Beer, pp. 1–4120.
- GRAF, D.L. & CUMMINGS, K.S. 2007. Preliminary review of the freshwater mussels (Mollusca: Bivalvia: Unionoidea) of Northern Africa, with an emphasis on the Nile. *Journal of the Egyptian German Society of Zoology* **53D**: 89–118.
- GRAF, D.L., GHAMIZI, M., KRISTENSEN, T.K., STENSGAARD, A.-S. & VAN DAMME, D. 2009. *Mutela dubia*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- GRAF, D.L., JØRGENSEN, A., VAN DAMME, D. & KRISTENSEN, T.K. 2011. The status and distribution of freshwater molluscs (Mollusca). In: Brooks, E.G.E., Allen, D.J. & Darwall, W.R.T., eds, *The Status and Distribution of Freshwater Biodiversity in Central Africa*. Cambridge, UK and Gland, Switzerland: IUCN, pp. 48–61.
- GRYSEELS, B., NKULIKYINKA, L., KABAHIZI, E. & MAREGEYA, E. 1987. A new focus of *Schistosoma mansoni* in the highlands of Burundi. *Annales de la Société belge de Médecine tropicale* **67**: 247–257.
- HUBENDICK, B. 1951. *Recent Lymnaeidae: their variation, morphology, taxonomy, nomenclature, and distribution*. Stockholm: Almqvist & Wiksells Boktryckeri.
- JICKELI, C.F. 1874. *Fauna der Land- und Süßwasser-Mollusken Nord-Ost-Afrika's*. Dresden: E. Blochmann.
- 1881. Land- und Süßwasser-Conchylien Nordost-Afrika's gesammelt durch J. Piroth. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft* **8**: 336–340.
- JØRGENSEN, A. 2008a. *Gabbiella humerosa*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- 2008b. *Potadoma ignobilis*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- 2008c. *Potadoma liricincta*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 06 July 2011)
- JØRGENSEN, A., JØRGENSEN, L.V.G., KRISTENSEN, T.K., MADSEN, H. & STOTHARD, J.R. 2007a. Molecular phylogenetic investigations of *Bulinus* (Gastropoda: Planorbidae) in Lake Malawi with comments on the topological incongruence between DNA loci. *Zoologica Scripta* **36**: 577–585.
- JØRGENSEN, A., KRISTENSEN, T.K. & STOTHARD, J.R. 2007b. Phylogeny and biogeography of African *Biomphalaria* (Gastropoda: Planorbidae), with emphasis on endemic species of the great East African lakes. *Zoological Journal of the Linnean Society* **151**: 337–349.
- JØRGENSEN, A. & VAN DAMME, D. 2009. *Ceratophallus kigeziensis*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- KORNIUSHIN, A.V. 1998. Notes on the anatomy of some species of *Sphaerium* s. l. (Mollusca, Bivalvia) from the tropical regions with revision of their taxonomic status. *Vestnik Zoologii* **32**: 3–12.

- 2004. A revision of some Asian and African freshwater clams assigned to *Corbicula fluminalis* (Müller, 1774) (Mollusca: Bivalvia: Corbiculidae), with a review of anatomical characters and reproductive features based on museum collections. *Hydrobiologia* **529**: 251–270.
- KORNIUSHIN, A.V. & GLAUBRECHT, M. 2006. Anatomy and reproduction of viviparous *Pisidium* (*Parapisidium*) *reticulatum* Kuiper, 1966: Implications for the phylogeny of Sphaeriidae (Mollusca: Bivalvia: Heterodonta). *Organisms Diversity & Evolution* **6**: 185–195.
- KRAUSS, F. 1848. *Die südafrikanischen Mollusken: Ein Beitrag zur Kenntniss der Mollusken des Kap- und Natallandes und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten*. Stuttgart: Ebner & Seubert.
- KUIPER, J.G.J. 1966. Les espèces africaines du genre *Pisidium*: leur synonymie et leur distribution (Mollusca, Lamellibranchiata, Sphaeriidae). *Annales de Musée Royal de l'Afrique Centrale, Série in 8°, Sciences Zoologiques* **151**: 1–78.
- KYAMBADDE, R. 2004. *Biomphalaria smithi*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- LANGE, C. 2004. *Biomphalaria stanleyi*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- LANGE, C.N. & VAN DAMME, D. 2009. *Pisidium kenianum*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- LEE, T. & Ó FOIGHIL, D. 2003. Phylogenetic structure of the Sphaeriinae, a global clade of freshwater bivalve molluscs, inferred from nuclear (ITS 1) and mitochondrial (16S) ribosomal gene sequences. *Zoological Journal of the Linnean Society* **137**: 245–260.
- LOREAU, M. & BALUKU, B. 1987. Population dynamics of the freshwater snail *Biomphalaria pfeifferi* in eastern Zaire. *Journal of Molluscan Studies* **53**: 249–265.
- MADHYASTHA, A. 2010. *Melanoides tuberculatus*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.1. (www.iucnredlist.org; accessed 15 September 2011)
- MANDAHL-BARTH, G. 1954. The freshwater mollusks of Uganda and adjacent territories. *Annales du Musée Royal du Congo Belge Série in 8°, Sciences Zoologiques* **32**: 1–206.
- 1957a. Intermediate hosts of *Schistosoma*: African *Biomphalaria* and *Bulinus*: I. *Bulletin of the World Health Organization* **16**: 1103–1163.
- 1957b. Intermediate hosts of *Schistosoma*: African *Biomphalaria* and *Bulinus*: II. *Bulletin of the World Health Organization* **17**: 1–65.
- 1967. Revision of the African genera *Potadoma* Gray and *Potadomoides* Leloup, and description of a new species of *Cleopatra* (Gastropoda Prosobranchia: Melaniidae). *Revue de Zoologie et de Botanique Africaines* **76**: 110–131.
- 1968. Revision of the African Bithyniidae (Gastropoda Prosobranchia). *Revue de Zoologie et de Botanique Africaines* **78**: 129–160.
- 1988. *Studies on African freshwater bivalves*. Charlottenlund: Danish Bilharziasis Laboratory.
- MARTENS, E., v. 1879. Ueber mehrerlei ausländische Conchylien. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin Juli*: 99–105.
- 1897. Beschalte Weichthiere Ost-Afrikas. In: Stuhlmann, F., ed., *Deutsch-Ost-Afrika*. Berlin: Dietrich Reimer, pp. 1–308.
- MICHEL, A.E., COHEN, A.S., WEST, K., JOHNSTON, M.R. & KAT, P.W. 1992. Large African lakes as natural laboratories for evolution: examples from the endemic gastropod fauna of Lake Tanganyika. *Mitteilungen. Internationale Vereinigung für Theoretische und Angewandte Limnologie* **23**: 85–99.
- MÜLLER, O.F. 1774. *Vermivm terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaceorum, non marinorum, succincta historia*. Volumen alterum. Havniæ & Lipsiæ: Heineck & Faber.
- OLIVIER, G.A. 1804. *Voyage dans l'Empire Ottoman, l'Egypte et la Perse, II*. Paris: Henri Agasse.
- PFENNINGER, M., REINHARDT, F. & STREIT, B. 2002. Evidence for cryptic hybridization between different evolutionary lineages of the invasive clam genus *Corbicula* (Veneroidea, Bivalvia). *Journal of Evolutionary Biology* **15**: 818–829.
- PIECHOCKI, A. 1993. Zairian population of *Pisidium viridarium* Kuiper, 1956 (Bivalvia: Heterodonta: Sphaeriidae). *Annales Zoologici* **44**: 55–63.
- PIECHOCKI, A. & KORNIUSHIN, A.V. 1994. Description of the anatomy of the two African pill clams: *Pisidium viridarium* Kuiper, 1956 and *P. kenianum* Preston, 1911 (Bivalvia Pisidioidea). *Malakologische Abhandlungen Staatliches Museum für Tierkunde Dresden* **17**: 57–64.
- PILSBRY, H.A. & BEQUAERT, J. 1927. The aquatic molluscs of the Belgian Congo, with a geographical and ecological account of Congo malacology. *Bulletin of the American Museum of Natural History* **53**: 69–602.
- POLI, G. 1791. *Testacea utriusque Siciliae eorumque historia et anatome*. Parmae: Regio Typographeio.

- PRESTON, H.B. 1910. Additions to the non-marine molluscan fauna of British and German East Africa and Lake Albert Edward. *Annals and Magazine of Natural History* **6**: 526–536.
- 1911. Descriptions of thirty-six new species of land and freshwater shells from British East Africa, chiefly from Mount Kenya and the neighbouring district. *Annals and Magazine of Natural History* **7**: 463–476.
- 1912. Diagnoses of new species of terrestrial and fluviatile shells from British and German East Africa, with the description of a new genus (*Eussoia*) from the Eusso Nyior River, BE Africa. *Proceedings of the Zoological Society of London* **82**: 183–193.
- SCHOLZ, H. & GLAUBRECHT, M. 2004. Evaluating limnic diversity: Toward a revision of the unionid bivalve *Coelatura* Conrad, 1853 in the Great Lakes of East Africa and adjacent drainage systems (Mollusca, Bivalvia, Unionidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe* **80**: 89–121.
- SCHULTHEISS, R., ALBRECHT, C., BÖSSNECK, U. & WILKE, T. 2008. The neglected side of speciation in ancient lakes: phylogeography of an inconspicuous mollusc taxon in lakes Ohrid and Prespa. *Hydrobiologia* **615**: 141–156.
- SCHULTHEISS, R., VAN BOCXLAER, B., WILKE, T. & ALBRECHT, C. 2009. Old fossils—young species: evolutionary history of an endemic gastropod assemblage in Lake Malawi. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **276**: 2837–2846.
- SCHULTHEISS, R., WILKE, T., JØRGENSEN, A. & ALBRECHT, C. 2011. The birth of an endemic species flock: demographic history of the *Bellamyia* group (Gastropoda, Viviparidae) in Lake Malawi. *Biological Journal of the Linnean Society* **102**: 130–143.
- SEEHAUSEN, O. 2006. African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **273**: 1987–1998.
- SENGUPTA, M.E., KRISTENSEN, T.K., MADSEN, H. & JØRGENSEN, A. 2009. Molecular phylogenetic investigations of the Viviparidae (Gastropoda: Caenogastropoda) in the lakes of the Rift Valley area of Africa. *Molecular Phylogenetics and Evolution* **52**: 797–805.
- SMITH, E.A. 1888. On the shells of the Albert Nyanza, Central Africa, obtained by Dr. Emin Pasha. *Proceedings of the Zoological Society of London* **56**: 52–56.
- 1906. Zoological results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunnington, 1904–1905. Report on the Mollusca. *Proceedings of the Zoological Society of London* **76**: 180–186.
- THIELE, J. 1911. Mollusken der deutschen Zentralafrika-Expedition. In: Schubotz, H., ed., *Wissenschaftliche Ergebnisse der deutschen Zentralafrika-Expedition 1907–1908*. Leipzig: Klinkhardt & Biermann, pp. 175–214.
- THIEME, M.L., ABELL, R., STIASSNY, M.L.J., SKELTON, P., LEHNER, B., TEUGELS, G.G., DINNERSTEIN, E., TOHAM, A.K., BURGESS, N. & OLSON, D. 2005. *Freshwater ecoregions of Africa and Madagascar: a conservation assessment*. Washington: Island Press.
- VAN DAMME, D. & VAN BOCXLAER, B. 2009. Freshwater molluscs of the Nile Basin, past and present. In: Dumont, H.J., ed., *The Nile: Origin, environment, limnology and human use*. Dordrecht: Springer, pp. 585–630.
- VAN DAMME, D. & PICKFORD, M. 2003. The late Cenozoic Thiaridae (Mollusca, Gastropoda, Cerithioidea) of the Albertine Rift Valley (Uganda-Congo) and their bearing on the origin and evolution of the Tanganyikan thalassoid malacofauna. *Hydrobiologia* **498**: 1–83.
- WILLIAMSON, P.G. 1981. Palaeontological documentation of speciation in cenozoic molluscs from Turkana Basin. *Nature* **293**: 437–443.
- WILSON, A.B., GLAUBRECHT, M. & MEYER, A. 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **271**: 529–536.