Freshwater Molluscs of the Nile Basin, Past and Present

Dirk Van Damme and Bert Van Bocxlaer

Abstract The malacofauna of the Nile is poor compared to that of the Congo and its degree of endemicity is lower. While the highest species richness of the Congo Basin is in stenotopic taxa that live in the rivers and lakes, the highest diversity in the Nile Basin occurs in eurytopic taxa living in fringe habitats such as temporary pools. The paucity of endemics that need perennial waters as well in the Lower Nile as in the White Nile confirms the geological evidence indicating instability and discontinuity in water supply during Plio-Pleistocene times.

The fauna of the Nile is predominantly Afrotropical in the Lower Nile and exclusively Afrotropical south of the junction of the White Nile and Blue Nile. Of all sub-basins, the degree of endemicity (either zero or two species) is lowest in the Equatorial Nile, indicating that the perennial aquatic environment in this sub-basin is young (probably Holocene) and lending support to the idea that the Bahr el Arab and White Nile Transcontinental Rift System were hydrologically unstable, with endorheic, alkaline lakes during most of the Plio-Pleistocene (Salama, 1997).

In the Lower (Egyptian) Nile and in the Ethiopian Highlands palaearctic faunal components occur, consisting of widespread species and of a limited number of endemics of palaearctic origin, related to Levantine species. Most of these taxa first appear in the fossil record around 2.5 Ma. There is no evidence that the Nile functioned as an invasion route for Eurasiatic species prior to that time. Only *Theodoxus niloticus* is possibly of Parathethyan origin and may have invaded in the Late Miocene. The main invasion of freshwater molluscs into Africa appears to have occurred via the Horn of Africa in Middle and Late Miocene times.

In the East African Rift, a diversified fauna occurs that only shares a fraction of species with the Nile Basin north of the Albert Nile (> ~5° N). In the equatorial headwaters, some species from southern Africa reach their northern limit, but the main community consists of species that are either endemic to one of the rift lakes or endemic to the region stretching from Turkana to the Kivu Basins. There hence exists a distinct East African bio-province, that was already recognisable in

D. Van Damme (✉) and B. Van Bocxlaer
Research Unit Palaeontology, Department Geology and Soil Science, Ghent University,
Krijgslaan 281 (S8), B-9000 Ghent, Belgium
e-mail: dirk.vandamme@ugent.be

Pliocene assemblages and that had developed before the present lakes formed in the Late Pleistocene. Concerning the young age of Lake Victoria and the occurrence of an endemic cichlid superflock in the lake, the fossil molluscan record points to a persistence in the East African Rift of freshwater bodies sufficiently extensive to harbour a molluscan community – and *ipso facto* also fish – during periods of aridity/hyperaridity. The hypothesis of Verheyen et al. (2003, 2004), that the stem lineages of the East African haplochromines, presently inhabiting Lakes Victoria, Kyoga, Rukwa, Albert, George, Edward and surrounding waters, already existed during the Late Pliocene is consistent with the fossil evidence. The location of the area(s) of refuge (around Mount Elgon?) remains hypothetic, however.

The fossil records of the Turkana Basin, Tugen Hills and Albertine Basin show that around the Miocene/Pliocene boundary, two distinctive tropical molluscan palaeo-bioprovinces existed in equatorial Africa: an East African and a Congolian province. Regular incursions in both provinces during the Pliocene by elements of a third group, the so-called 'Nilotic' community, indicate the presence of a third distinctive Afrotropical palaeo-bioprovince situated more to the north. The molluscan community of the Chad Basin contains the same 'Nilotic' species (or closely related forms) as found in the Egyptian and Sudanese Nile but is more diverse, particularly in unionoids. Considering the climatic instability in the region of the different Nile Basins north of ~5° NL, the Neogene Chad-Eosahabi/Palaeosahabi system *sensu* Griffin (2006) is considered the most likely region of origin of the 'Nilotic' malacofauna, while the southern part of the Chad Basin (Chari-Logone system) may have acted as a refuge of this 'Nilotic' fauna during arid phases.

During Late Pliocene and Pleistocene wet phases the White Nile may have contained a perennial hydrological system, creating opportunities of exchange of aquatic faunas with Chad and the East African Rift System.

1   Introduction

The taxonomy and ecology of the Modern freshwater gastropod fauna of the Nile basin is well known. Research on freshwater molluscs of the Lower Nile started 200 years ago by French explorers such as Guillaume-Antoine Olivier (1801–1807), Jules-Cesar Savigny, who made the figures for the natural history volume of the 'Description de l'Egypte' (see Audouin, 1826), and Fréderic Cailliaud (1826). The first large collections from the Great Rift lakes were made some 30 years later, in 1859 by John Hanning Speke (molluscs reported by Dohrn, 1864). But some parts of the Nile Basin, in particular the Sudd area in Southern Sudan and the Blue Nile-Awash watershed in the Ethiopian Highlands, only were explored as late as the second half of the twentieth century (Brown, 1965; Brown et al., 1984; Brown, 1994).

The fact that African freshwater snails were so intensely studied in these early days is not primarily related to the nineteenth century's fascination with the search for the Sources of the Nile but with the discovery, in the early twentieth century, that the freshwater snail genera *Bulinus* and *Biomphalara* are the intermediate hosts of trematodes causing human schistosomiasis (bilharziasis), a disease

afflicting tens of millions of people in the tropics. This induced the World Health Organisation to allocate funds for studying African freshwater molluscs. From 1950 onward, two research centres were established, the Experimental Taxonomy Division of the Natural History Museum, London and the Mandahl-Barth Research Centre for Biodiversity and Health (formerly the Danish Bilharziasis Laboratory), Copenhagen.

The results of the malacological investigations on gastropods were compiled by David Brown (NHM) in his monograph 'Freshwater snails of Africa and their medical importance' (Brown, 1980, 1994). In the last two decades funding for gastropod research has been divided among several parties, and the focus of the research shifted. Modern research on African gastropods is mainly directed at endemic species flocks inhabiting (putative) long-lived lake systems, such as L. Tanganyika, L. Malawi and L. Victoria, and their evolutionary importance (e.g., West et al., 2003; Wilson et al., 2004; Genner et al., 2007; Glaubrecht & Strong, 2007; Sengupta et al., 2007). This research follows in the wake of molecular investigations on lacustrine cichlid species flocks and the claim that these lakes are 'living laboratories of evolution' (Martens, 1997; Rossiter & Kawanabe, 2000). Overview articles treating the African representatives of a particular family (e.g., Jorgensen et al., 2008) unfortunately remain rare, making it difficult to establish relationships between species of different hydrological basins and between lacustrine and fluvial ones.

African freshwater bivalves, being virtually of no economic or medical importance, have, in comparison to gastropods, been far less investigated. The major taxonomic reference works are 'Studies on African freshwater bivalves' by Georg Mandahl-Barth (Mandahl-Barth, 1988) and a synoptic inventory by Daget (1998). Mandahl-Barth's study exemplifies the taxonomic concepts prevailing in western malacology during the second half of the twentieth century, viz. that most species described by earlier workers are ecophenotypic variations or geographic races of a limited number of polymorphic, widespread biospecies. As a result, the Afrotropical unionoids (59 species), as treated by Mandahl-Barth (1988), was the least diverse of all tropical naiad faunas. Although Mandahl-Barth's work remains important, his taxonomic views are no longer followed (Daget, 1998; Graf & Cummings, 2007a, b; Van Bocxlaer & Van Damme, in press; Van Damme pers. data). Reversal of the lumping trend is related to the sudden dramatic world-wide interest in freshwater bivalves, presently considered a central item in biodiversity research and conservation biology. There exist now a general consensus that the large unionoid bivalves are the group of freshwater organisms most vulnerable to environmental stress (Ricciardi & Rasmussen, 1999; Lydeard et al., 2004). The observation that they are decimating world wide at an alarming rate (70% of the 300 species in North America are extinct or red-listed) (Bogan, 1993, 1996) emphasises this clearly. The result is that African freshwater bivalve research at present mainly focuses on mapping biodiversity and classifying taxa. Whereas current freshwater gastropod research is mainly financed from an evolutionary perspective, the main funding for freshwater bivalve research is provided by wildlife conservation instances. In 2002, a Mussel Project (Musselp; Dr Daniel L. Graf and Dr Kevin S. Cummings) was set up, aimed at providing a global classification of unionoid diversity. This project unites the main unionoid collections of the world and is hosted by the USA

Academy of Natural Sciences (http://www.mussel-project.net/). With respect to the Nile, a team, in collaboration with the University of Cairo, is working on a research project named Mashrua Al Mahar, which studies the biodiversity of the unionoid fauna of the Egyptian Nile.

The IUCN is currently making threat assessments of the freshwater molluscs of the Nile Basin as part of the Pan Africa Biodiversity Project (2005–2009). A regional approach is being used; the malacofauna of the Great Lakes region is treated as part of the Eastern Africa Freshwater Biodiversity Assessment (Darwall et al., 2005), that of the Egyptian Nile will be treated in the assessment of Northern African, to be published in 2010 (Cuttelod et al., 2007), and that of the Mountain Nile, White Nile and Blue Nile in the Northeastern assessment (to be published in 2010).

Truly unique is the completeness of the African fossil record of Late Tertiary freshwater molluscs and the length and intensity of palaeontological investigations on the subject. Research was initiated in Egypt in the nineteenth century as part of the efforts to reconstruct the evolution of human civilisation along the Nile (von Martens, 1886; Germain, 1909). In the region of the Great Lakes, the earliest palaeontological investigations such as the Wayland Expedition and the Cambridge Expedition started in the Albertine Basin around 1920 but the interest in these rich fossil malacofaunas was minimal (Cox, 1926; Fuchs, 1934, 1936). In the 1970s, the African Rift Valley, in particular the Turkana Basin, produced impressive hominid finds and was acclaimed the cradle of mankind. A steep increase of research on other fossil groups followed (e.g., Harris et al., 1988; Leakey & Harris, 2003). The study of the fossil molluscs proved important not only for palaeoenvironmental reconstruction and biostratigraphy but it also yielded interesting insights in evolutionary processes (Williamson, 1981a, 1981b, 1990; Van Damme, 1984; Van Damme & Pickford, 1994, 1995, 1999, 2003; Van Bocxlaer & Van Damme, in press).

2   Composition of the Modern Nile Fauna in a Continental Perspective

About 58 genera of freshwater gastropods and 17 genera of freshwater bivalves occur in Africa, not taking into account the malacofauna of the Maghreb with its many endemic creno- and stygobiont hydrobiids (~15 genera) (Ghamizi, 1998), the endemic thalassoid paludomids (formerly thiarids) of Lake Tanganyika (~18 genera) (West et al., 2003) and those restricted to brackish waters (~20 genera) (Brown, 1994; Daget, 1998).

The Nile harbours about 25 gastropod genera (Table 1) and 11 bivalve genera (Table 2), which represent 43% and 65% of all African genera, as mentioned above (Brown, 1994; Daget, 1998; Graf & Cummings, 2007b). These are low percentages considering the geographical extent of the Nile Basin and the climatic zones it covers. Moreover, the basin includes a vast range of aquatic habitats and ecosystems,

Table 1 Freshwater Gastropods of the Nile, Chad and Turkana Basins

Species			Nile Basin			Chad Basin	Turkana Basin/ Omo Delta
		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region		
PROSOBRANCHIA							
Neritidae							
Theodoxus niloticus	E/P	X	?				
Viviparidae							
Bellamya unicolor		X	X	X	X	X	
Bellamya phthinotropis	E				Vi		
Bellamya costulata	E				Vi		
Bellamya jucunda	E				Vi		
Bellamya constricta	E				Vi		
Bellamya trochlearis	E				Vi		
Bellamya rubicunda	E				Al		
Ampullariidae							
Pila ovata		X			X	X	
Pila wernei				X		X	Om
Lanistes carinatus		X		X	X		
Lanistes ovum				X		X	
Valvatidae							
Valvata nilotica	E/P	X	X				
Hydrobiidae							
Hydrobia ventrosa	P	X					
Hydrobia musaensis	E/P	X					

(continued)

Table 1 (continued)

Species		Lower Nile	Nile Basin			Chad Basin	Turkana Basin/ Omo Delta
			Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region		
Pomatiopsidae							
Tomichia sp. n.	E						Tu
Bithyniidae							
Gabbiella humerosa complex					X		
Gabbiella senaariensis	E	X		X		X	
Gabbiella kichiwambae	E				X		
Gabbiella parva	E				X		
Gabbiella schweinfurthi	?E			X			
Gabbiella barthi	E				X		
Gabbiella candida	E				Al		
Gabbiella walleri	E				Al		
Gabbiella neothaumiformis	E					X	
Gabbiella tchadiensis	E					X	
Gabbiella rosea	E						Tu
Thiaridae							
Melanoides tuberculata		X	X	X	X	X	Om, Tu
Pleuroceridae							
Cleopatra bulimoides		X	X	X	X	X	Om
Cleopatra sp. indet	?E						Tu
Cleopatra guillemei					X		
Cleopatra cridlandi	E				Vi		
Cleopatra hemmingi							X
Potamididae							
Pirenella conica		X					
PULMONATA							

Taxon						
Lymnaeidae						
Lymnaea natalensis	Int		X	X	X	X
Lymnaea columella	P	X				
Lymnaea truncatula	P	X				
Lymnaea stagnalis	P	X				
Ancylidae						
Ancylus fluviatilis	P/Mnt	X	X	X		
Ancylus regularis	E/P/Mnt	X	X			
Burnupia edwardiana	E				Ed	
Burnupia stuhlmanni	E				Vi	
Ferrissia isseli		X	X	?		
Ferrissia clessiniana	?E	X				
Ferrissia l'hotelleriei	?E	X				
Ferrissia pallaryi	?E	X				
Ferrissia kavirondica	E				Vi	
Ferrissia eburnensis					X	X
Planorbidae						
Planorbis planorbis	P	X				
Afrogyrus coretus		X	X	X	X	X
Armiger crista	P/Mnt		X			
Ceratophallus natalensis			X		X	X
Ceratophallus kigeziensis				?	X	Tu
Ceratophallus kisumiensis	E				Vi	
Ceratophallus bicarinatus			X		Al	X
Ceratophallus subtilis	E				Vi	
Ceratophallus concavus	E				Vi	

(continued)

Table 1 (continued)

Species		Nile Basin				Chad Basin	Turkana Basin/ Omo Delta
		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region		
Ceratophallus crassus	E				Vi		
?Ceratophallus apertus	E				Ed		
?Ceratophallus faini	E				Al		
Gyraulus costulatus		X	X	X	X	X	
?Gyraulus sp. indet.							Tu
Lentorbis junodi				X	X	X	
Segmentorbis angustus		X	X	X	X	X	Tu
Segmentorbis eussoensis				X	?		
Segmentorbis kanisaensis				X		X	
Biomphalaria pfeifferi			X	X		X	
Biomphalaria choanomphala	E				Vi, Al, Ky		
Biomphalaria elegans	E				Al		
Biomphalaria smithi	E				Ed		
Biomphalaria stanleyi	E				Al	X	
Biomphalaria alexandrina	E	X		X			
Biomphalaria sudanica				X	X	X	
Biomphalaria tchadiensis	E					X	
Helisoma duryi	Int	X					
Bulinus africanus			X		X		
Bulinus nasutus					X		
Bulinus jousseaumei						X	
Bulinus ugandae			X		X		

Bulinus umbilicatus							X
Bulinus obtusus							X
Bulinus hexaploidus	Mnt			X			
Bulinus octoploidus	Mnt			X			
Bulinus transversalis	E					Vi	
Bulinus trigonus	E					Vi, Ed	
Bulinus natalensis/tropicus com				X	X	X	
Bulinus truncatus				X	X	X	X
Bulinus permembranaceus	Mnt		X			X	
Bulinus forskalii			X	X	X	X	X	X
Bulinus scalaris				X		X	
Bulinus reticulatus				X		X	
Physidae							
Physa acuta	Int	X	X	X			
Total n species	92	29	25 (26)	21 (23)	50 (51)	27	11
Total Palaearctic species	11	8	4 (5)	0	0	0	0
Total montane species	6	0	5	0	1	0	0
Total endemic species	37 (42)	5 (8)	2 (3)	1?	27	3	2 (4)
Total introduced species	3	3	1	0	0	0	0

Abbreviations: E: endemic; P: Palaearctic; Int: introduced; Mnt: montane; Al: L. Albert & Albert Nile; Ed: Lake Edward; Ky: Lake Kyoga; Om: Omo Delta; Tu: Lake Turkana; Vi: Lake Victoria.

Table 2 Freshwater Bivalves of the Nile, Chad and Turkana Basins

Species			Nile Basin			Chad Basin	Turkana Basin/ Omo Delta
		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region		
UNIONOIDA							
Unionidae							
Unio abyssinicus	E/P/Mnt		X				
Unio dembeae	P		X				
Coelatura aegyptiaca		X		X	X	X	Om
Coelatura gabonensis						X	
Coelatura bangoranensis	E					X	
Coelatura bakeri	E				Al, Ed		
Coelatura stuhlmanni	E				Al, Ed		
Coelatura hauttecoeuri complex	E				Vi, Ky		
Coelatura aliuaudi	E				Vi		
Coelatura cridlandi	E				Vi		
Nitia teretiuscula	E	X		X		X	
Nitia monceti	E				Vi		
Nitia acuminata	E			?	Al		
Nitia chefneuxi (extinct?)	E						?Om
Nitia mutelaeformis	E					X	
Iridinidae (=Mutelidae auct.)							
Aspatharia chaiziana				X		X	
Aspatharia pfeifferiana						X	
Aspatharia marnoi	E			X			
Aspatharia divaricata	E			X	Vi		
Chambardia rubens		X		X		X	

Taxon						
Chambardia wismanni					X	
Chambardia wahlbergi		X		X	X	Om
Chambardia tabula		X			X	
Chambardia letourneuxi	E	X				
Chambardia trapezia	E			Vi, Al, Ed		
Chambardia bourguignati	E			Vi		
Mutela dubia		X	X	Al, Ed	X	Om
Mutela joubini					X	
Mutela rostrata		X	X	Al, Ed	X	Om
Mutela bourguignati	E			Vi		
Mutela alluaudi	E			Al, Ed		
Etheriidae						
Etheria elliptica			X	X	X	Om
VENEROIDA						
Corbiculidae						
Corbicula fluminalis		X	X	X	X	Om,?Tu
Pisidiidae (=Sphaeriidae auct.)						
Sphaerium hartmanni complex		X	X	X	X	
Sphaerium victoriae complex				Vi, Al, Ed		
Sphaerium stuhlmanni	E			Vi		
Sphaerium regulare	E			Vi		
Sphaerium nyanzae	E			Vi		
Pisidium pirothi		X	X	X	X	
Pisidium fistulosum	E			Vi		
Pisidium amnicum	Int	X	X			
Pisidium kenianum			X			
Pisidium armillatum	Mnt				X	
Pisidium invenustum	Mnt				X	

(continued)

Table 2 (continued)

Species		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region	Chad Basin	Turkana Basin/ Omo Delta
				Nile Basin			
Pisidium montigenum	Mnt				X		
Pisidium ethiopicum	E/Mnt		X				
Pisidium casertanum	P		X		X		
Pisidium subtruncatum	P						
Eupera ferruginea		X	X	X	X	X	
Eupera crassa	E				Vi		
Total n species:	51	12	11	13 (14)	32	18	6 (7)
Total Palaearctic species	4	4	3	0	1	0	0
Total montane species	5	1	2	0	3	0	0
Total endemic species	25	3	2	2 (3)	16	2	1?
Total introduced species	1	1	0	0	0	0	0

Abbreviations: E: endemic; P: Palaearctic; Int: introduced; Mnt: montane; Al: L. Albert & Albert Nile; Ed: Lake Edward; Ky: Lake Kyoga; Om: Omo Delta; Tu: Lake Turkana; Vi: Lake Victoria.

encompassing a large river delta that connects to the Mediterranean palaearctic zone, a lower Nile surrounded by desert, several extensive artificial lakes, e.g., Lake Nasser, a drowned upper Nile with extensive swamps and floodplains in tropical lowland (the Sudd) and montane bogs and the extensive lake Tana in the Ethiopian Highlands, large equatorial rift lakes such as Lake Albert, Lake Edward and Lake Victoria and glacier lakes on the Rwenzoris (Thieme et al., 2005).

When a comparison of the mollusc fauna of the two largest African freshwater systems, the Nile and the Congo, is made at species level, the low diversity of the Nile becomes even more obvious. The Nile is the second largest drainage system of Africa, only surpassed by the Congo (Goudie, 2005). Compared to the Nile, the habitats in the Congo Basin are less diversified, consisting mainly of rainforest rivers and large rift lakes (Thieme et al., 2005). Brown (1994), comparing the species richness of the fluvial snail faunas of the Nile and Congo Basins with exclusion of the large lakes, pointed out that the number of gastropods known from the Nile Basin is about half that of the Congo, namely 51 to 96 species (taking *Ferrissia* and *Burnupia* into account as genera only) and the proportion of endemics is much lower, namely 10 out of 51 species. In bivalves, biodiversity is equally lower in the Nile Basin, with a total of 28 species versus 38 in the Congo drainage. The degree of bivalve endemism is dramatically lower in the Nile Basin with only 5 endemic species compared to 18 in the Congo Basin (Daget, 1998; Graf & Cummings, 2007a, b).

Moreover, the molluscan faunas of both basins have a significantly different community composition (Fig. 1), reflecting important ecological differences. In the Congo Basin prosobranch snails and unionoid bivalves are overwhelmingly dominant, while in the Nile Basin pulmonate snails and pea and basket mussels (Sphaeriidae and Corbiculidae) are more abundant. Concerning gastropods, the ratio prosobranchs to pulmonates is 74/22, thus >3/1, in the Congo Basin, while in the Nile Basin this ratio is reversed, namely 15/36 or <1/2. For bivalves, the ratio unionoids to veneroids in the Congo Basin is 25/10 while in the Nile Basin it again is reversed, namely 13/18.

A contrast in species richness between the Nile and Congo Basins can also be observed in the brackish water faunas; the relative poverty of the Nile fauna is apparent. In the oligohaline to mesohaline waters of the Congo estuary six gastropod genera (*Neritina, Hydrobia,*?*Potamopyrgus* (probably a distinct genus), *Tympanotonus*, *Pachymelania* and the pulmonate *Melampus*) and two bivalve genera (*Egeria* and *Iphigenia*) occur, one *Egeria* species being endemic (Pilsbry & Bequaert, 1927; Brown, 1994; Daget, 1998). In the oligo- to mesohaline part of the Nile estuary two gastropod genera (*Hydrobia, Pirenella*) and two bivalves (*Cerastoderma* and *Scrobicularia*) occur. None are endemic (Van Damme, 1984).

The two African basins are hence inhabited by what is essentially a different molluscan community. The explanation for this phenomenon becomes clear when the reproduction, the dispersal strategies and the habitat preferences of the diverse groups (Fig. 1) are taken into consideration.

African freshwater prosobranchs have separate sexes and reproduce via cross-fertilisation, except for parthenogenetic *Melanoides* and hermaphroditic *Valvata* (Brown, 1994). Prosobranchs are viviparous, ovoviviparous or oviparous (Brown,
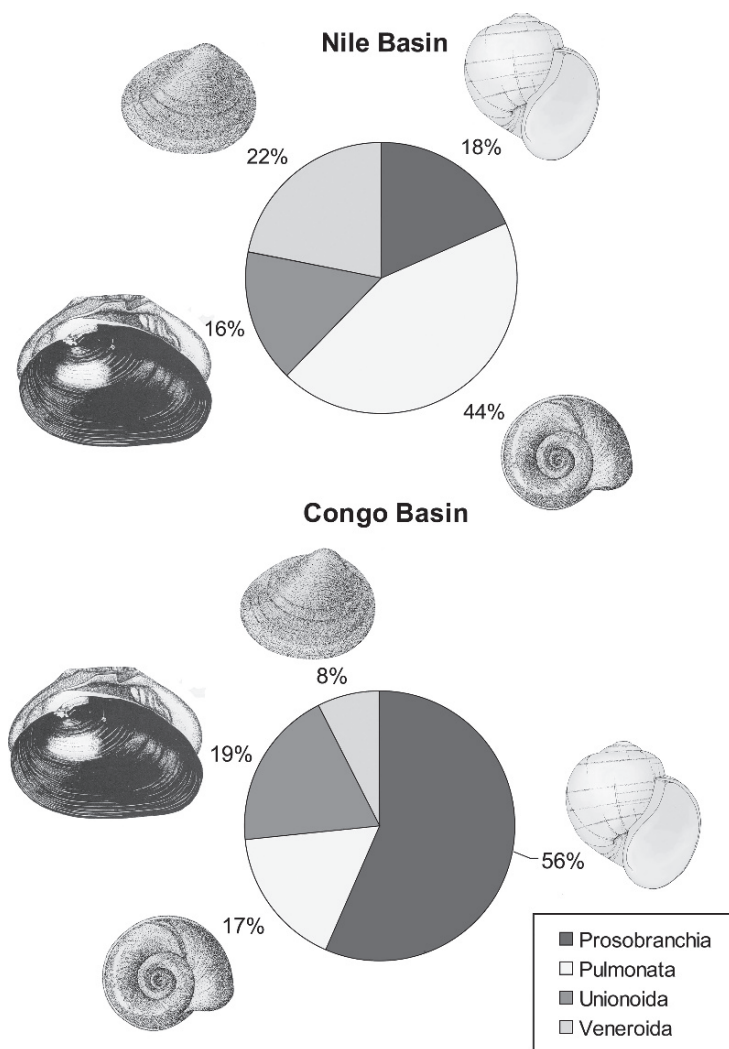
Fig. 1 Taxonomic differences at a high hierarchical level in the composition of the malacofauna of the Nile and Congo Basins.

1994) and the number of young produced is usually limited. The young have generally a cryptic lifestyle, hiding in the sediment or between vegetation. Prosobranch species are gill-breathers. Most have a relatively thick shell and operculum, protections against predators. They are benthic or endobenthic organisms that favour well oxygenated habitats and colonise open substrates in rivers and lakes along a vertical gradient from the littoral to sizeable depths (over −50 m). Dispersal capacities of most prosobranchs are low, except for the parthenogenetic and hermaphroditic taxa, due to their mode of reproduction and life style (Van Damme, 1984; Brown, 1994).

African unionoids (Unionidae, Iridinidae, Etheriidae) also reproduce sexually, breath through gills and live in the sediment (endobenthic) except for the river oyster *Etheria elliptica*, which lives cemented to hard substrates. They have adapted their reproductive strategies to life in freshwater streams and rivers by two important aspects, viz. parental care and parasitism. Both counteract the unidirectional drag to the ocean by river currents that planktonic larvae would experience (Graf & Cummings, 2006). Since active dispersal capacities are limited in unionoid bivalves, their dispersal capacity is mainly determined by the dispersal capacities of their fish host. Many unionoids are highly selective as to the type of sediment they settle in. They also tend to aggregate as a result of their mode of reproduction and limited active dispersal capacities, so that populations can be strongly localised (Van Damme, 1984).

African pulmonates are hermaphroditic and oviparous (Van Damme, 1984). They have no operculum, a fragile shell and a mantle cavity that serves as an air-breading organ (lung), lacking true gills (Brown, 1994). They hence stay close to the water surface, avoiding turbulent waters and have difficulties in colonising depths. Pulmonates favour shallow waters with aquatic vegetation, on which they depend not only for protection but also for food (they are microfeeders scraping off Aufwuchs) and for reproduction, i.e., the deposition of their egg clusters (Brown, 1994). In general, pulmonates inhabit more marginal, less stable (both in terms of longevity and water conditions) water bodies than prosobranchs. Due to their reproductive strategy and the fact that their eggs (1 to 100 per cluster) are encapsulated in a drought resistant, gelatinous substance, they easily disperse via zoochory.

Corbiculid mussels are known for their great invasive potential, partly induced by their wide spectrum of reproductive strategies (Glaubrecht et al., 2006). Sphaeriid mussels are self-fertilising hermaphrodites that developed parental care via brooding, producing viviparous, crawl-away juveniles (Park & Ó Foighil, 2000; Korniushin & Glaubrecht, 2006). Juvenile pea clams (Sphaeriidae) do not only live on the bottom but crawl on plants using their sticky foot. They also are easily dispersed by water birds and water insects, clutching at their legs and feathers (for an overview on zoochorous dispersal see Van Damme, 1984 and Wesselingh et al., 1999).

The Congo Basin is hence inhabited by a molluscan fauna with high species richness in benthic or endobenthic K-strategists, while in the Nile system the number of K-strategists is limited and that of r-strategists is markedly higher. The most speciose group in the Nile is the family Planorbidae, particularly well-represented by the genus *Bulinus*. This taxon can be used as an example of diversification and speciation in the Nile basin, because it has been intensely studied (see Brown, 1994). *Bulinus* is highly eurytopic, excelling in exploiting all kinds of stagnant waters such as small seasonal water bodies, pools in floodplains, artificial ponds, dams, etc. and is not well presented in flowing waters and lakes. Moreover, *Bulinus* is able to survive droughts. Reproduction occurs by both cross-fertilisation (outcrossing) and self-fertilisation (selfing). While outcrossing, maintaining heterogeneity in a population, seems to be preferred; virgin individuals introduced zoochorously in newly formed pools will successfully self-fertilise (Brown, 1994). Brown (1994) suggested that the ability of self fertilisation, resulting in numerous 'biotypes' with

different fixed heterozygous loci, probably gave rise to polyploidy. *Bulinus* species originally are diploid, but the extremely successful and eurytopic *B. truncatus*, is tetraploid. *Bulinus truncatu*s has a considerable aestivation capacity and is a successful colonist of all kinds of artificial biotopes such as irrigation systems and man-made lakes as far north as Portugal, Sardinia and Corsica and as far south as the DRC and Congo. Other polyploids, namely the tetraploid *B. membranaceus*, the hexaploid *B. hexaploidus* and the octoploid *B. octoploidus* are adapted to high altitudes (Kenyan mountains, Ethiopian highlands). From this evidence Brown (1994) postulated that polyploidy enabled *Bulinus* to extend successfully to extremely altered/stressed habitats as well as to colder regions, i.e. Mediterranean Europe and the Afrotropical montane region.

Most of the malacofauna of the Nile Basin – except for that of the large lakes – did not originate by diversification and speciation within the river and its tributaries *sensu stricto*, but via founder effect divergence in temporary waters after faunal exchange (via hydrological contacts) with the main hydrographic system. In contrast, the malacofauna of the Congo Basin diversified *in situ* in streams. The fundamental difference in natural history, diversity and evolution of the malacofaunas of the two largest African Basins reflects a difference in environmental stability. The Congo fauna is the product of selection and speciation in a stable environment since Miocene times (Goudie, 2005), favouring diversification in K-selective stenotopic taxa with a low to modest dispersal capacity. Speciation, according to the distribution patterns observed, occurred within fluvial habitats, e.g., either in tributaries that temporally became geographically or ecologically isolated from the rest of the hydrographic network or in surface waters of smaller basins that became subsequently connected. The Nile Basin on the other hand represents a much less stable hydrological system, that suffered major changes during its Cenozoic history, with the birth of the modern Nile happening only ~25 ka ago (Issawi & McCauley, 1992; Goudie, 2005). The Nile fauna, as such, is the product of selection and speciation in a highly instable and stressed environment, which favoured diversification in r-selective eurytopic taxa with high dispersal capacities.

3   Cenozoic History of the Nile Basin and Its Molluscan Fauna

3.1   Oligocene Times

During Oligocene times, part of the area occupied at present by the Nile Basin may have been occupied by the Qena river system, flowing initially west and subsequently southwest (Goudie, 2005). Though numerous Oligocene molluscan sites are known from northern Africa (Mauritania to Egypt and Sudan), no fossils indicative for the presence of a large river have been recovered. The malacofauna is extremely poor, consisting – with exception for one planorbid snail (gen. sp.

indet.) – exclusively of ampullariids (*Lanistes, Pila, Pseudoceratodes*) (Van Damme, 1984). This monotonous fauna of air-breathing snails indicates that the dominant palaeo-environment during that period was tropical stagnant swamp with conditions similar to the present Sudd. During the Oligocene, the Arabian Peninsula was breaking away from Africa (Schattner et al., 2006). In the region of Thaytiniti (Oman) a molluscan fauna of Oligocene age (corresponding to the Fayum L 41 level, Martin Pickford, pers. comm.) has also been discovered but unfortunately only perfunctorily sampled. On the Arabian Peninsula, ampullariids indicative for the same paludinal palaeo-environment as in the Qena Basin, are equally dominant, but the marked compositional differences on genus and on species level do indicate a geographic separation between the faunas of eastern Arabia and northern Africa and little exchange between both regions in the Oligocene (Van Damme, pers. data).

3.2   Miocene Times

Fossil exchange during the early Miocene is poorly documented. Some freshwater gastropods may have invaded from tropical Asia, such as e.g. *Melanoides*. Fossil assemblages in the northern part of the East African Rift indicate that most molluscan genera recently occurring in the Afrotropics were already present in the Middle Miocene, some possibly having arrived from Eurasia in earlier times. The Late Cenozoic (Early Miocene to present) history of the Afrotropical malacofauna is best recorded in deposits of the East African Rift System, namely in the Albertine Basin (Uganda-Congo) (Adam, 1957, 1959; Williamson, 1990; Morris, 1995; Van Damme & Pickford, 1994, 1995, 1999, 2003), the Turkana Basin (Kenya-Ethiopia) (Williamson, 1981a, 1981b; Van Damme, 1984; Williamson, 1985; Van Bocxlaer et al., 2008; Van Bocxlaer & Van Damme, in press), the Tugen Hills (Central Kenya) and Rushinga Island (L. Victoria, Kenya) (Van Damme, 1984; Pickford, 1986; De Groeve, 2005). All these regions are, or were once part of the Nile Basin.

During the Late Miocene, between ~8.0 and 5.4 Ma (Late Tortonian and Messinian stages) northern Africa and Arabia experienced a humid phase (the Zeit Wet Phase) due to the initiation of the Asian/African monsoon ~8.0 Ma (Griffin, 1999, 2002; Böhme, 2004). At the onset of that wet phase the Eonile (Said, 1981, 1993) arose. Originally, this was a modest river not reaching far beyond the Egyptian-Sudanese border. But during the Messinian salinity crisis ~5.96–5.33 Ma, the Mediterranean dried out and brackish lakes formed on the bottom (Krijgsman et al., 1999). The Eonile eroded an impressive canyon from Aswan till the Mediterranean floor with a width varying between 10 and 20 km and a depth of 170 m at Aswan and 2,500 m north of Cairo (Said, 1993; Butzer, 1999; Griffin, 1999). At the end of the Messinian stage the Eonile ended in the oligohaline Palaeolake Cyrenaica, at the bottom of the eastern Mediterranean (Issawi & McCauley, 1992; Griffin, 1999, 2002; Goudie, 2005; Griffin, 2006). The last stage of this palaeolake is better known as Lago Mare (~5.5 Ma), since most deposits are located in Italy.

A major part of Modern African fish families were first recorded in the Late Miocene, namely the Osteoglossidae, Mormyridae, Gymnarchidae, the barbid genus *Barbus*, Distichodontidae, Characidae, most Bagridae, Tetraodontidae and Schilbeidae (Stewart, 2001). Channidae were considered to have crossed from Eurasia during this period (Böhme, 2004) but a recent discovery of Oligocene remains in Egypt (Murray, 2006) contradicts this, suggesting that the observed pattern could be due to preservational bias.

It has been suggested that the major Late Miocene invasion route between Eurasia and Africa for freshwater organisms was via the above-mentioned Mediterranean palaeolake southwards into Africa via the Eonile (e.g., Stewart, 2001, based on fish distribution). The molluscan record does not confirm this (see Heller, 2007 for an in depth discussion). During the Late Messinian, the Eonile had formed a deep canyon. Similar modern canyon rivers confined within vertical walls, with denuded rocky bottoms, and additionally with seasonal water fluctuations are poor migration routes for benthic prosobranchs and endobenthic unionoids. This is exemplified by their absence from the Grand Canyon of the Colorado river (USA) (Spamer & Bogan, 1993), from the gorge of the Blue Nile (Brown, 1994), and from the rapids of the Matadi-Boma Channel (Lower Congo), where only rheophilous gastropods adapted to adhere to rocks and the cementing river oyster *Etheria elliptica* occur (Brown, 1994; Graf, pers. comm., 2007). A second argument is the absence of Paratethyian molluscs in north-eastern Africa. This conspicuous absence remains a major zoogeographic riddle (Heller, 2007). Palaeolake Cyrenaica/Lago Mare was fed by water from the more eastward located brackish/freshwater Euxinian and Pannonian palaeolakes (Dacic Basin) (Magyar & Sztanó, 2007) and was inhabited by a highly typical Pannonian euryhaline community consisting of Neritidae, Thiaridae, Melanopsidae, Hydrobiidae, Cardiidae (of the endemic subfamily Limnocardiinae) and Dreissenidae (Esu, 2006). Remnants of this Paratethyian fauna, in particular species of the genus *Melanopsis*, different hydrobiid genera, and *Psilunio* presently occur all around the Mediterranean Basin. The main exception is the Mediterranean rivers in a region from Libya east to Sinai (Heller, 2007). The presence of the abovementioned genera in the rivers around the western Mediterranean proves that these Pannonian molluscs succeeded in moving from Palaeolake Cyrenaica stream upwards, reaching the parts of river basins that presently lie above sea level. The absence of Pannonian relicts in Quaternary deposits of the Nile system suggests that in contrast to the rest of the Mediterranean basins, either the Eonile was not colonised by a Pannonian malacofauna, or that all traces of this fauna were subsequently wiped out (though the Pannonian molluscs were/are highly eurytopic). No Afrotropical fossils have yet been found in the rich Lago Mare deposits nor inversely have any Paratethyian fossils been recorded from north-eastern African deposits. This suggests that, in contrast to the basins in the Maghreb, the Iberian Peninsula, Italy and the Levant, there was limited interchange of malacofaunas between the palaeo-lake Cyrenaica/Lago Mare and the river systems of north-eastern Africa (Eonile and Palaeosahabi). A possible exception may be the snail *Theodoxus niloticus* (Neritidae), endemic to the lower Nile (and Blue Nile?). This species is euryhaline and rheophilous, and may have been able

to invade the canyon of the Eonile via Palaeolake Cyrenaica. Brown (1994) states that *T. niloticus* appears closely related to *T. jordanicus* from the Levant. This is correct, but does not automatically imply a recent arrival in Africa, certainly since representatives of the Neritidae are morphologically conservative and possess a limited number of diagnostic features. A last argument against the Palaeolake Cyrenaica-Eonile as an invasion route is the discrepancy in time. The palaeotropical freshwater molluscs that invaded Africa during the Late Miocene appear around 7–6 Ma in the fossil record, i.e. before the Messinian Salinity Crisis took place. The appearance of the Asiotropic unionids in Africa hence occurred at a time when the Mediterranean was still a sea, and hence a barrier.

Reconstructions of the palaeo-environment and tectonic events in the Ethiopian Rift during the Late Miocene–Early Pliocene (Redfield et al., 2003) show the existence of a broad connection (the Danakil Isthmus) between Yemen and Ethiopia in Miocene times. South of that land bridge, a string of lakes and rivers stretched out along the axis of the Danakil-Awash valley towards Kenya (Redfield et al., 2003). Environmental conditions in the region of the Horn of Africa during the Late Miocene were hence suitable for molluscan invaders (e.g. the unionid genus *Pseudobovaria*; Van Damme pers. data) while conditions in the Mediterranean-Eonile region were not, and those in the Sinai-Gulf of Suez region were suboptimal, with playa-like brackish waters/badland conditions (Griffin, 1999).

3.3 Pliocene Times

In the early Pliocene, water levels in the Mediterranean rose, and the canyon of the Eonile became a marine gulf extending as far south as Aswan. This marine gulf phase separates the earlier Eonile stage and the subsequent Palaeonile stage *sensu* Said (1981). The latter can be defined as the period during which a freshwater river again extended north to the region of Cairo. The Palaeonile was a regional river that did not extend beyond Egypt and supposedly was active from ~4.0 till 1.8 Ma, i.e., almost during the whole Pliocene epoch (Said, 1981; Butzer, 1999). A long and continuous active phase appears however unlikely in the light of our present knowledge of the climatological dynamics and the occurrence of marked dry/wet phases in Pliocene eastern Africa (Trauth et al., 2005).

The Pliocene-Early Pleistocene palaeo-hydrography of the Nile Basin in regions south of Egypt remains poorly documented and the reconstruction summarised below remains conjectural. It is assumed by Salama (1987, 1997, 2005) that a series of endorheic basins had formed along the axis of an ancient rift in the region at present occupied by the White Nile. These basins are suggested to have contained episodic shallow and alkaline palaeolakes extending from the Sudd till southern Kordofan. Salama (2005) recognises from south to north eight of such closed lake basins: (1) Palaeolake Sudd, fed by the Bahr el Arab, the White Nile and the Sobat River, (2) Palaeolake Adar with the Adar river, (3) Palaeolake Nuba, fed by the khor Abu Habil, (4) Palaeolake Gezira in which some rivers from the Ethiopian

Highlands ended (including the Blue Nile?), (5) Palaeolake Atbara with the Atbara River, (6) Palaeolake Gash with the Gash River, (7) Palaeolake Bayuda, fed by the Wadi El Melik and the Wadi El Mogaden and (8) Palaeolake El Qaab in which the Wadi Howar discharged. At what periods these lakes existed and whether they existed simultaneously is unknown. According to Salama (2005) is it possible that these shallow alkaline lakes, situated in the 'Intercontinental Rift', became inter-linked (and fresh) during wet phases. According to this scenario a Pliocene White Nile may have formed intermittently during the Late Pliocene-Early Pleistocene, establishing an aquatic migration route not only in north-south direction but equally in a west–east sense, i.e. between the Chad Basin and the Turkana Basin (see further). As to the existence of a Pliocene Blue Nile, if such a river existed, it probably did not run north-westwards to the Nile Basin but eastwards to the Red Sea (Goudie, 2005).

Still more to the south, the area of the Great Lakes drained west into the Palaeo-Congo, the continental divide being situated along the western shoulder of the Gregory rift (Van Damme & Pickford, 2003; Goudie, 2005). The main drainage east of this rift shoulder was in a north-south direction. It consisted of the Palaeo-Omo river, originating on the Ethiopian Plateau, the Turkwell-Kerio system and the Palaeo-Turkana river *sensu* Feibel (1999), a vast system that reached the Indian Ocean at the equator (see Fig. 2).

No fossil assemblages of Pliocene age are known from the Nile Basin in Egypt and Sudan. However, 'Nilotic' faunas, i.e. faunas that consist for an important part of species presently occurring in the White Nile and the Nile, appear in the Turkana Basin and Albert Basin at several stages during the Pliocene. These provide evidence of the molluscan fauna that existed north of these basins. The appearance of these Nilotic invaders, e.g., *Valvata* sp., and *Coelatura aegyptica* (Van Bocxlaer et al., 2008), in the Turkana Basin coincides with a wet phase ~2.0–1.8 Ma that was not confined to the basin only (Brown & Feibel, 1991) but was widespread over East Africa (Trauth et al., 2005). In the Albertine Basin similar invasions occurred around that time (Van Damme & Pickford, 1994, 1999). These data hence seem to corroborate Salama's hypothesis.

The 'Nilotic' invaders of tropical origin (not the palaeartic ones such as *Valvata*) may have originated in the region of the Chad Basin, actually using the Sudanese Nile as intermittent stepping stone during wet phases (see further). The appearance during Pliocene times (from ~3 Ma onward) of Palaeartic taxa closely related or identical to species occurring in the Levant (e.g., *Unio dembeae, Corbicula flu-minalis*) indicates that a new hydrographic connection had been established with Eurasia. Since the Street of Bab el Mandeb, connecting the Red Sea with the Indian Ocean has been open from around 4.5 Ma till the present (Redfield et al., 2003), the only possible invasion route was via the Sinai. These invaders, being cold water taxa, must have followed the Levant-Sinai-Nile route during wet but relatively cold phases. During the Late Pliocene, species belonging to the tropical snail genera *Bellamya* and *Melanoides* are also found in Levantine deposits (Sivan et al., 2006; Heller, 2007). These species may hence have followed the same Sinai-corridor out of Africa during wet but relatively warm phases. However, since the genera *Bellamya*
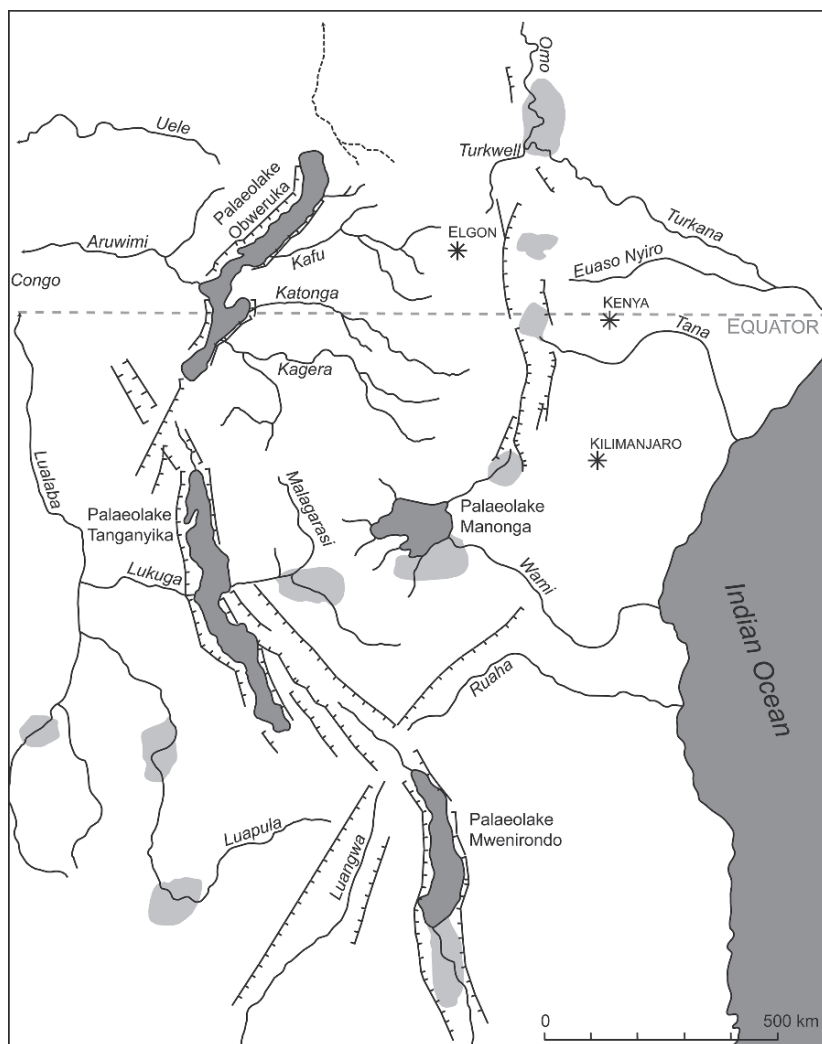
Fig. 2 Hydrographical configuration in the Great African Rift region in the Early Pliocene (ca 4 Ma). A large and deep rift lake in the Albertine Basin, Palaeolake Obweruka, started to divide into a southern and a northern basin by the rising Rwenzori Horst. Palaeolake Tanganyika may either have already reached its present configuration (as is figured) or may still have been confined to the Southern Basin of the Tanganyika Trough. Both lakes at that time drained westwards to the Congo. Early Pliocene Palaeolake Mwenirondo was probably confined to the northern Livingstone Basin, possibly extending in the Ushishya Basin of the Malawi Trough (as is figured). The region of present Lake Victoria was drained by rivers flowing westward to Palaeolake Obweruka. South of this drainage the shallow Palaeolake Manonga filled the Wembere-Manonga Basin (max. depth: ~20–30 m) (Tanzania), draining eastwards towards the Indian Ocean. In the Turkana region, the Palaeo-Omo meandered through a shallow basin (intermittently filled with short-lived lakes) southwards to the Indian Ocean via the now defunct 'Turkana River'. The coastal outline of East Africa represented in the figure does not take into account marine transgressions during that period (after Van Damme & Pickford, 2003). Light grey zones indicate swamps and temporal lakes.

and *Melanoides* are actually better represented in tropical Asia than in Africa, they may have invaded the Levant from the Iranian region (Heller, 2007). There is no indisputable evidence that the Nile or the Sinai land bridge ever was used by fresh water molluscs for dispersal northwards, in contrast to a considerable number of (non-primary) freshwater fish (Goren & Ortal, 1999).

3.4   *Pleistocene – Modern Times*

During an early Pleistocene dry phase, from ~1.7 Ma, the Palaeonile in Egypt became a seasonal river (wadi) (Goudie, 2005), and finally ceased flowing. After this dry phase, around 1.5 Ma, the Protonile *sensu* Said (1981) was formed but, as its predecessors, it remained largely confined to Egypt. It is only in the mid-Pleistocene, around 700 ka that the first extensive Nile system, the Prenile *sensu* Said (1981), came into existence. It was fed by water from southern Sudan and from the Ethiopian Highland as, due to a tilting of the Ethiopian plateau, the Atbara and Blue Nile started flowing north and westwards rather than to the Red Sea (Goudie, 2005). The Prenile pushed into Egypt across the Nubian Swell by a series of cataracts. This vast river existed until ~200 ka, when hyperarid conditions set in and perennial flow ceased. About 120 ka ago, the Neonile *sensu* Said (1981), significantly less vigorous than the Prenile, originated (Goudie, 2005). Due to tectonic changes, the region of the Great Lakes tilted northward around 30,000–25,000 BP (Pickford et al., 1993) and became part of the Nile catchment.

With the help of modern dating techniques, in particular thermoluminescence, the complex palaeohydrography/limnology of the Nile basin during these Middle and Late Pleistocene times has been largely elucidated. During wet phases, respectively around 400, 320–250, 240–190, 155–120, 90–65 and 10–5 ka, corresponding with Marine Isotope Stage (MIS) 11, 9, 7, 6/5e, 5a or 5c and the Holocene wet phase, the Protonile and the Late Pleistocene-Holocene Neonile were (re)activated and extensive endorheic lakes as well as lakes connected with the Nile (Fayum lakes) formed in Egypt (Szabo et al., 1995; Churcher et al., 1999; Smith et al., 2004, 2007). Further southwards along the axis of the basin of the White Nile a palaeolake with a length of >500 km formed around 400 ka and there is evidence for several very high White Nile stands between 250 and 15 ka (Williams et al., 2001, 2003; Salama, 2005). During intermittent arid phases, the Nile became wadi-like, in particular during the Glacial Maximum around 16,000 BP, as mentioned above. The present hydrographic system came into existence around 12,000 BP when Lake Tana, Lake Victoria and Lake Albert, after having dried out during the last hyperarid phase, spilled over into the Blue, the Victorian and the White Nile (Goudie, 2005).

The fossil record from the Fayum depression, Kom Ombo, Bir Tarfawi, Bir Sahara, Kurkur Oasis, Kharga, Nubia and Kordofan, shows that during Middle to Late Pleistocene times the molluscan fauna was essentially the same as the present one (see Van Damme, 1984 for a detailed overview). The only difference is the

ratio Palaearctic/Afrotropical species, which fluctuates with temperature. It should be pointed out that, with one exception in Lower Egypt, no fossil assemblages have been found that consist exclusively of palaearctic or afrotropical species (Van Damme, 1984). It would hence appear that temperatures, at least during the periods from which molluscan assemblages are known, did not descend below those occurring presently on the Ethiopian plateau, nor did they become too high to sustain palaearctic species.

The Late-Pleistocene or Holocene Nile deposits do not show evidence that the equatorial malacofauna from the Great Lakes region dispersed north into the White Nile after a hydrographic connection was established. On the contrary, during the Holocene some 'Nilotic' species, such as *Coelatura aegyptiaca* and *Mutela dubia,* did penetrate as far south as Lake Albert (Graf & Cummings, 2007b) and as far east as the Omo River delta, although not into Lake Turkana itself (Van Bocxlaer & Van Damme, in press).

3.5 Where Did the Nilotic Malacofauna Originate and Where Did It Survive During Hyperarid Phases?

The Late Cenozoic evolution of the palaeohydrography and palaeohydrology of the Nile Basin, sketched above, shows that the aquatic ecosystems in the Nile basin were highly unstable partly due to tectonic changes and mainly due to climatologic shifts. The absence of endemic Afrotropical molluscs in the Nile Basin north of the Great Lake region, except for two or one species of *Chambardia* that are able to aestivate during dry periods (see further), confirms the lack of persistence of perennial waters trough time.

In northeastern Africa, north of ~5° N, conditions were unsuitable for the evolution and persistence of groups such as unionoids and prosobranchs that presently populate the Nile (see discussion Congo/Nile fauna). Yet the fossil record indicates that a typical 'Nilotic' malacofauna existed and persisted from the Early Pliocene onward. These two statements appear to be contradictory, but it should be noted that the term 'Nilotic' is biogeographically misleading since this concept indicates similarities between faunas occurring in the Nile, the Chad, the Niger and the Senegal Basins, in contrast to e.g. faunas with Congolian affinities. Since the Nile is the largest African river it was implicitly assumed by former researchers (e.g., Huckriede & Venzlaff, 1962) that during the former African 'Pluvial Stages', the 'Nilotic' fauna had invaded these other basins from the Nile. The African Pluvial/Interpluvial chronological concept used by these authors, analogous to the Glacial/Interglacial stages, has been completely abandoned.

The presently available geological data make the hypothesis of a Plio-Pleistocene Nile as a centre of faunal diversity highly questionable. But if not from the Nile Basin, where did the 'Nilotic' fauna come from? Of all the basins mentioned above, the Niger Basin has the lowest percentage of 'Nilotic' species; less than one third of its modern gastropod fauna is shared with the Nile

Basin (Brown, 1994). The Ethiopian Highland and the Blue Nile are improbable candidates as region of origin and refuge, due to their climatologic instability and because a connection between the Ethiopian Highland and the Nile was established only during the Middle Pleistocene (Goudie, 2005). The Senegal Basin equally is situated in a highly unstable climatologic, semi-arid zone. Therefore, the Chad Basin, in which a molluscan fauna highly similar to the one of the Nile Basin but richer occurs, seems the most probable candidate as region of origin and as refuge. Griffin (1999, 2002, 2006) reported that during the Late Miocene a hydrographical system composed of the Palaeo-Chari/Logone + Neogene Lake Chad + the Eosahabi/Palaeosahabi rivers formed the longest (>3,000 km) and most important north-south directed river system in Africa for more than 2 million years (from 7.0 to ~4.5 Ma). During the early Messinian the Palaeosahabi exited Neogene L. Chad in the northeast to join the Eonile via the Mourdi Depression. Later, during the drawdown phase, the Eosahabi eroded a channel in which the present Ounianga lakes are located, winding northwest towards the Gulf of Sirt (Libya) where it cut a canyon of 396 m (Griffin, 2002, 2006). Though the size of Neogene Lake Chad (maximal extension = 700,000 km^2) and hence the amount of water flowing north into the Sahabi system appears to have been dependent of the precessional Milankovitch cycle (Krijgsman et al., 1999), the Chadian hydrographic system was during the Late Miocene and Early Pliocene the only long-lived system where the distinctive 'Nilotic' fauna could have developed. This suggestion is in agreement with the (disputed) hypothesis of Lihoreau et al. (2006) concerning the existence of a separate Chado-Libyan aquatic palaeobioprovince in the late Miocene. According to Lihoreau et al. (2006), the amphibian mammal fauna (anthracotherids, hippotamids) discovered in the late Miocene deposits of Toros-Menella (Northern Chad) is clearly distinctive from the East African one (e.g., from the Turkana Basin), evidencing hydrographical discontinuity between these regions at that time (see also Griffin, 2006).

During the remainder of the Pliocene and during the Pleistocene, with increasing aridity, the Sahabi system degraded, while more to the east, the Palaeonile and subsequently the Protonile evolved (see above). Although the Chadian Basin was likely too shallow to harbour a lake during hyperarid periods, the headwaters of some of its tributaries, such as the Chari and Logone, are situated so far south in the tropical rainforest belt that the Chadian molluscan community must have persisted there during arid times. During wet periods this fauna may not only have extended northwards again into the Chad Basin but may also have invaded the Nile Basin via the shallow watershed divide between the Chari and the Bahr el Arab south of Jebel Marra (from where the White Nile-Sudd Basin could be re-colonised) or via the divide of the Bahr el Gazal with the Wadi Howar northeast to the Nile in Egypt. Another possibility would be via the so-called Radar Rivers *sensu* McCauley et al. (1982) (see also Issawi & McCauley, 1992). These rivers channels, revealed under the Great Selima Sand Sheet by radar shuttle, were initially considered to run in a south-westward direction, forming a Nile-Chad connection during the Late Cenozoic. However, the direction of this drainage system has been disputed and in addition there is no way to date this system(s) (Goudie, 2005).

In conclusion it can be stated that the 'Nilotic' malacofauna probably did originate around the onset of the Pliocene in what Lihoreau et al. (2006) call the Chado-Libyan palaeobioprovince and that the area of refuge during hyperarid phases were the southern headwaters of the Chad Basin.

3.6   The Vanished Long-Lived Lakes in the Nile Basin, Their Thalassoid Malacofauna and Their Contribution to the Equatorial Malacofauna

According to the geological and biological evidence the lakes in the Albertine Basin, i.e., L. Albert and L. Edward, are young, namely about 25,000 years and their ecosystems may well be much younger (Pickford et al., 1993). The degree of endemism in their molluscan faunas is low as are the morphological differences with the malacofauna of the Albert and White Nile, into which these lakes drain. These inconspicuous differences are quite recent. From about 7.5 till 2.5 Ma a giant rift lake, Palaeolake Obweruka (surface: 27,000 km^2), persisted in the Albertine Basin that during most of its existence paralleled present Lake Tanganyika (present surface area: 32,900 km^2, present maximum depth: 1470 m) in size, depth and general configuration (see Fig. 2). Both lakes originated during the same geological time, the Late Miocene, were about 300 km apart and were part of the palaeo-Congo drainage. Of prime interest for malacology is that both stand faunistically completely apart from all other recent and all known former African lakes because of the presence of a thalassoid malacofauna.

As in Lake Tanganyika, the molluscs of Palaeolake Obweruka have a peculiar marine-like appearance. The strange marine-like (= thalassoid) gastropods of Lake Tanganyika have fascinated geographers and biologists since John Hanning Speke presented them to the Royal Geographic Society in 1859. They were promptly used as prime evidence by the proponents of the theory that Lake Tanganyika was a part of the Tethys Sea that had become landlocked during the Jurassic (Moore, 1903). Since, these notions have been proven erroneous. Lake Tanganyika has an estimated age of about 7 Ma, and the marine-like morphology of its molluscan inhabitants evolved via convergence. The studies on neogene African lakes indicate that Palaeolake Obweruka is the only African lacustrine system known with an age equal to that of Lake Tanganyika and in which a thalassoid malacofauna developed. Lakes such as present Lake Victoria, Albert and Edward whose ecosystems have an age in the range of 10,000 to 20,000 years, or modern L. Malawi, whose physical-chemical conditions have only become suitable for freshwater molluscs since 95 to 130 ka ago (Cohen et al., 2007), are exclusively inhabited by malacofaunas that show modest degrees of divergence from their ancestral fluvial morphotypes.

In the decades following the marine origin debate, different proposals about the causality of the exorbitant shell ornamentation of the Tanganyikan shells were advanced. The predator-prey arms race hypothesis is the latest one (West et al., 1991;

West & Cohen, 1994). The ongoing controversy presently centres about the question if the thalassoid lineages evolved in the lake from a single non-thalassoid ancestor (monophyletism or at best paraphyletism) (West & Michel, 2000) or if the different thalassoid lineages originated well before the formation of Lake Tanganyika (polyphyletism) in the Palaeo-Congo system and subsequently invaded the nascent Lake Tanganyika (Wilson et al., 2004). The two hypotheses are of equal value since, by lack of a fossil Tanganyikan record, neither can be substantiated.

In the light of this controversy and its consequences for the evolution of freshwater biota, a brief summary of the fossil record of Palaeolake Obweruka is here represented, constituting direct evidence of tempo and mode in an extremely long-lived African lake.

3.6.1   Palaeolake Obweruka I (7.5 to 4.5 My)

Geological and fossil evidence indicates that extensive lakes existed in the Albertine Basin from the onset of the rifting (around 15 Ma), but evidence for a deep and permanently stratified rift lake (anoxic deep water clays) only emerges around 8–7.5 Ma (Pickford et al., 1993).

The molluscan and fish fauna found in the earlier deposits of Palaeolake Obweruka clearly are derived from those that existed in the precursor lakes. From the onset, the evolutionary patterns in these two biota are markedly different. In the fish fauna a major evolutionary event occurred during the earliest stage. It resulted in the appearance of several endemic, molluscivorous genera, namely *Bunocharax* (Characidae), with huge molariform crushing teeth and *Nkondobagrus*, a bagrid catfish with a strongly elongated and heavily ossified snout (Fig. 3) (Van Neer, 1994; Van Damme & Pickford, 2004). Equally abundant are representatives of the bagrid genus *Chrysichthys*, molluscivores that apparently swallow rather than crush molluscs (Van Damme, pers. obs., 2008, based on stomach contents of *Chrysichthys* from the Sanaga R. in Cameroon).

Despite the evidence for the presence of abundant molluscivorous fish, the dominant gastropod lineages, belonging to the Viviparidae and Paludomidae, which represent ~95% of the community, do show only a modest degree of morphological changes, similar to the type found in most modern African lakes. The development of extremely ornamented morphologies was restricted to some relatively rare species, e.g., the unique, spinose *Lanistes senuti* (Ampullaridae). Even within the Ampullaridae these armoured species – hence putatively better adapted to predation – appear to have only represented a minor fraction of the biomass, i.e. <5%. The low response to predation in the abundant molluscan species and the dramatic response in a few rare species in the presence of a strongly diversified molluscivore community appears to challenge the conventional concepts of arms-race theory (Vermeij, 1987).

Between 4.5 and 4.0 Ma, a marked disconformity in the stratigraphic sequence, indicating a lake level drop, was reported (Pickford et al., 1993). In the deposits postdating this disconformity a dramatic change in the composition of the molluscan
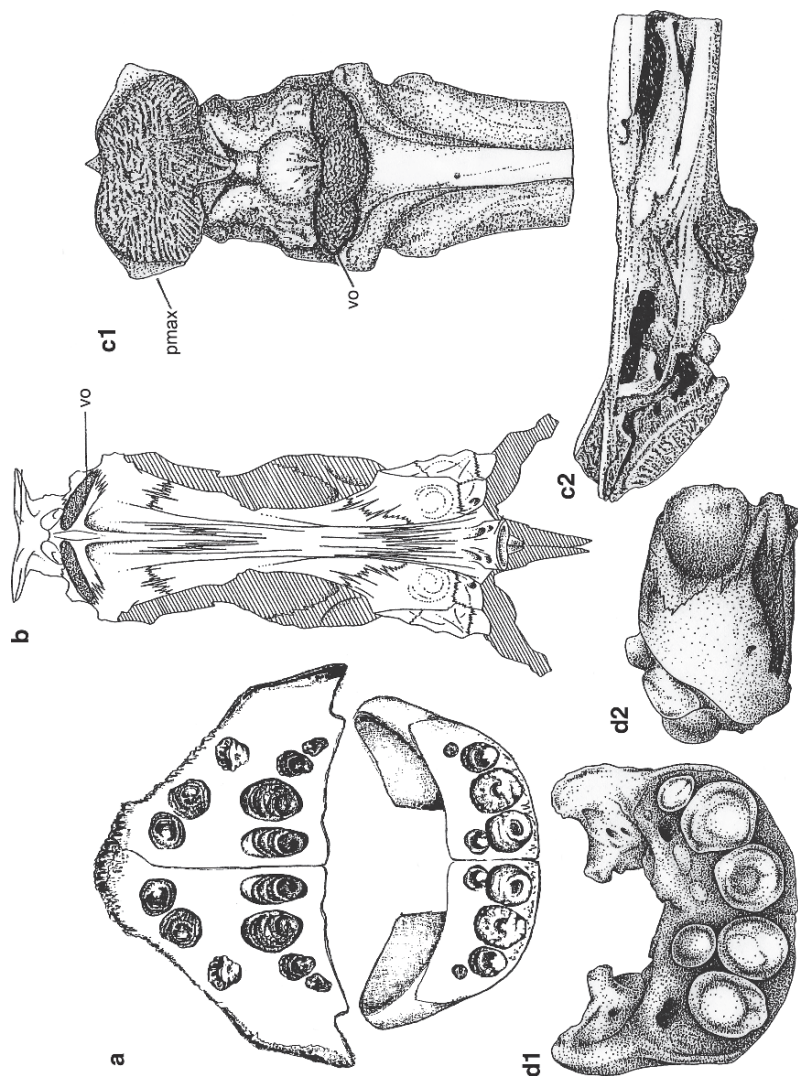
Fig. 3 Some fossil molluscivorous fish genera from the Albertine and Turkana Basins: (**a**) *Sindacharax* (Characidae), total length: 20–220 cm; widespread, common in all palaeolakes of the Turkana Basin and in Palaeolake Lusso (Albertine Basin); extinct. (**b**) *Chrysichthys* (Bagridae). Total length: 30–150 cm. widespread, extant. (**c**) *Nkondobagrus* (Bagridae), total length ≥50 cm, catfish with strongly ossified shovel-like snout, endemic to Palaeolake Obweruka, extinct. (**d**) *Bunocharax* (Characidae), total length >70 cm, endemic to Palaeolake Obweruka, Kaiso and Lusso, extinct (after Van Damme & Pickford, 2003).

assemblages was observed (Van Damme & Pickford, 1995, 1999, 2003). A severe extinction event, mainly in benthic organisms (such as molluscs and crabs) is evidenced by the fact that only a few surviving endemics (2 gastropods and 1 bivalve) are recovered, and all early thalassoids are absent. Co-occuring with the scant survivors, representatives of new invasive taxa (e.g. the Pachychilid *Potadoma*) appear in the strata of Palaeolake Obweruka II, that reached the size of Palaeolake Obweruka I (Van Damme & Pickford, 1995, 1999, 2003).

3.6.2   Palaeolake Obweruka II (4.0 to 2.5 Ma)

Shortly after the flooding of Palaeolake Obweruka II, a marked and rapid radiation did occur in each and every gastropod taxon, survivors as well as invaders, resulting in a highly diverse malacofauna composed exclusively of thalassoids. Some surviving genera (e.g. *Neothauma*), unornamented during Palaeolake Obweruka I produced the highest variability in ornamentation ever observed in a molluscan species flock (ribs, carinae and spines; Van Damme & Pickford, 1999). The stunning ornamentation, produced simultaneously in several genera can only be explained as an intensive reaction to predation (Vermeij, 1987; West & Cohen, 1994). It remains unexplained why all gastropods developed highly armoured shells, while the dominant molluscivourous fish taxa are the same as those inhabiting Palaeolake Obweruka I. The surviving lineages apparently possess the genetic possibility to produce ornamented shells, but why did this not occur before in Palaeolake Obweruka I? From the ensuing two million years an apparently unilateral armsrace with gastropods becoming increasingly more armoured is documented (Van Damme & Pickford, 1999, 2003) (Fig. 4).

3.6.3   Palaeolake Kaiso and Palaeolake Lusso (2.5 to 2.0 Ma)

The final chapter of this fascinating evolutionary story initiates around 2.5 Ma, when the rise of the Ruwenzori Horst broke up Palaeolake Obweruka. The two remnant lakes, Palaeolake Kaiso and Palaeolake Lusso, occupied the basins in which respectively Lake Albert and Lake Edward are situated at present. The palaeolakes were somewhat larger then their modern counterparts, and both were still part of the Congo catchment.

   After a last phase of intense morphological changes, mainly restricted to the pachychilid genus *Potadoma*, the ecosystems of Palaeolakes Kaiso and Lusso were drastically altered. Between 2.3 and 2.0 Ma the remaining endemic lineages of molluscs and fish were replaced by a widespread malacofauna, erroneously termed 'Nilotic' by former authors (Adam, 1957, 1959; Gautier, 1970).

   Comparing the fossil evidence of Palaeolake Obweruka to the hypotheses on the origin of the Tanganyikan thalassoids, we can conclude that several (at least 4) paludomid and pachychilid lineages invaded the lake independently.
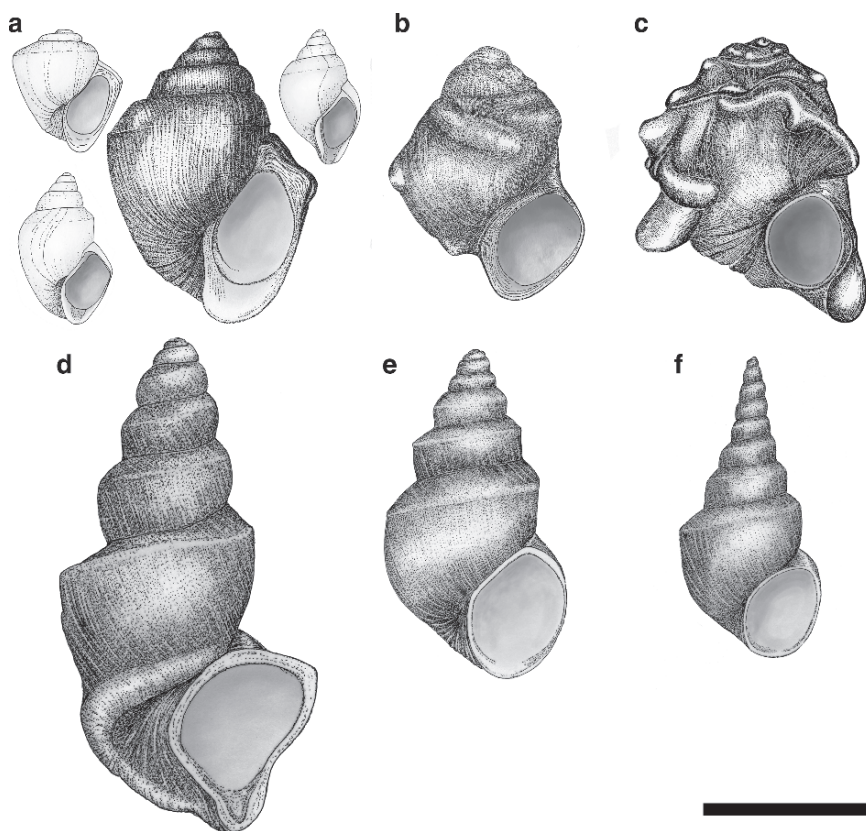
Fig. 4 The genus *Potadoma* (Pachychilidae): modes of conchyological evolution in African lakes. (**a–c**) Example of thalassoid evolution: an unornamented and thin shelled *Potadoma* species (*P. sebugoroensis*) gives rise to the extremely ornamented and thick *P. brevissima*. This evolution took place in long-lived Palaeolake Obweruka (Albertine Basin) over a period of ~2 million years (from 4.5 till 2.5 Ma). Such intense changes are only observed in the extremely long-lived lakes Obweruka and Tanganyika. (**d–f**) Example of non-thalassoid evolution: the fluvial *P. lomekwiensis*, with slowly but continuously enlarging whorls, evolves to *Potadoma* sp. nov., with a shell that grows first in length and subsequently rapidly enlarges in whorl size. This evolutionary development took place in the relatively short-lived Palaeolake Lokeridede (~50 ka) that existed in the Turkana Basin around 2.5 Ma. Such modest shell alterations, e.g. a shorter or smaller spire and/or weak ornamentation, are observed in all other present and former lakes, regardless of predation pressure. Included in this second group is Palaeolake Lorenyang (Turkana Basin) with an estimated age of 300 ka and hence 'long-lived' according to the prevailing definition of >100 ka (Rossiter & Kawanabe, 2000). Scale bar is 10 mm.

The thalassoid cerithioids in Palaeolake Obweruka were thus, corroborating the claim of Wilson et al., 2004 for Lake Tanganyika, likely not monophyletic. However, in Palaeolake Obweruka, the fossil evidence leaves no doubt that the invading lineages became thalassoid after having invaded the lake, as was equally proposed for the Tanganyikan fauna by West and Michel (2000). Although the

most likely explanation is indeed that thalassoidism is a response to predation, the fossil record of Palaeolake Obweruka also indicates that the massive presence of specialised molluscivorous predators does not *in se* trigger a significant response, and other important factors must come into play as well.

Another interesting question is whether molluscs, originating in long-lived lakes, may subsequently spread in the hydrographical system, hence is intralacustrine evolution a main agent for maintaining diversity on the scale of a hydrographic basin or a region? In the case of Palaeolake Obweruka, the answer appears to be negative; none of the many endemics did spread outside the lake. Apparently, intralacustrine evolution in a 'long-lived' system may lead to a dead end. The most interesting conclusion that can be drawn from the Obwerukan fossil record is that in a large long-lived lake such as Palaeolake Obweruka (and by extension Lake Tanganyika) ecological insulation from the surrounding water bodies (incoming rivers, swamps, . . .) is established rapidly after the formation of the lake. Except for the invasion following the extinction event that terminated Palaeolake Obweruka I, the degree of eco-insularity appears to have been absolute (Van Damme & Pickford, 2003). A similar neat separation between lake ecosystem *sensu stricto* and fringe habitats has been noted for Lake Tanganyika. Parthenogenetic and extremely eurytopic and opportunistic species, e.g., the Asiatic species *Corbicula fluminalis*, which spread over Africa about 2.8 Ma ago (Van Bocxlaer et al., 2008), are still absent from Lake Tanganyika (Leloup, 1950).

4   Modern Biogeographic Regions of the Nile Basin

Within the Nile Basin four regions can be discerned on differences in the molluscan communities as on hydrogeological characteristics, namely:

  – the Lower Nile in Egypt and North Sudan
  – the Blue Nile – Lake Tana – Ethiopian Highland
  – the Mountain Nile – Sudd – White Nile
  – the Great Lakes

4.1   *The Lower Nile in Egypt and North Sudan*

This region is the part of the river extending northwards from the junction of the White Nile with the Blue Nile to the Nile Delta (Fig. 5). The most recent inventory of the malacofauna of the Egyptian part of this region is by Ibrahim et al. (1999). This study is valuable because it is the first time that the Nile has been sampled so intensively, but the taxonomy of the bivalves unfortunately is based on nineteenth century authors of the Ecole Nouvelle. The malacofauna of the Lower Nile can be discerned from that of the other regions by the presence of Palaearctic taxa. Some of these, e.g., *Lymnaea stagnalis*, *L. auricularia*, *Planorbis planorbis*, are widespread

in the Palaearctic region. During the Early Holocene they occurred further south but presently they are restricted to the freshwater part of the Nile Delta (Van Damme, 1984), from which they are rapidly disappearing due to climate change (Van Damme pers. data). Five Palaearctic species are endemic, either to the Lower Nile or to the Ethiopian Highland (Tables 1 and 2). According to Brown (1994) the endemic Palaearctic snails *Theodoxus niloticus*, *Valvata nilotica* and *Gyraulus ehrenbergi* are closely related to and perhaps co-specific with Levantine species. The southern range extension of these palaearctics did fluctuate considerably during the Late Pleistocene – Holocene. During colder wet phases all these species extended as far south as northern Sudan and *Valvata nilotica* fossils are even found in the Chad Basin and the Turkana Basin, in the latter appearing for the first time around 200–150 ka (Bume Formation) (Van Damme, 1984). Two palaearctic unionids, *Unio abyssinicus* and *U. dembeae*, have presently disappeared from the Lower Nile but were abundant during the Late Pleistocene-Early Holocene cold phases. These species still occur in the Blue Nile – Lake Tana – Ethiopian Highland region and in part render the faunal community of this region distinctive (see below). Though *U. dembeae* was considered to belong to the circum-Mediterranean *Unio elongatulus* (presently *U. mancus*) complex (*U. elongatulus dembeae*) (Daget, 1998), it is probably better to consider it distinct till further research on this complex provides more information.

The number of Afrotropical endemics in the Lower Nile is extremely low (Table 1 and 2). There is only one putative speciose group, the *Ferrissia iselli* complex, with five species endemic to the Nile basin, of which three are endemic to the Lower Nile. The diversification within these small pulmonates may represent another example of rapid speciation through founder-effect, as in *Bulinus*, but it is more likely that molecular analysis will show that the genetic distinction is low or non-existing. We share the opinion of Brown (1994) who considers the number of African *Ferrissia* species to be '*highly uncertain; many are founded on shell differences but probably few are really distinct, for shell shape seems to be related to current speed and type of substratum*'. A low degree of genetic diversification has also been demonstrated for the African *Biomphalaria* representatives. All African species of this pulmonate genus cluster closely together with one South American species, *B. glabrata* (Campbell et al., 2000; Morgan et al., 2002). The taxonomic distinctiveness of *Biomphalaria alexandrina*, a species 'endemic' to the Upper and White Nile is hence rather spurious. The only solid endemic Afrotropical species of the Lower Nile appears to be the naiad *Chambardia letourneuxi* (Iridinidae), confined to the delta and probably extinct (Graf & Cummings, 2007b). It should be pointed out that many representatives of the genus *Chambardia* can aestivate and that the presence of this endemic is therefore not necessarily indicative for perennial waters.

Concerning the malacofauna of the brackish part of the Nile Delta and the saline coastal lakes we refer to the study of Barash and Danin (1992) on the coastal molluscs of Israel and Sinai, since the community composition is identical. Only a few brackish water species are found deeper inland, e.g. in the saline lake Birket Qarun, namely *Hydrobia musaensis, Pirenella conica, Cerastoderma glaucum*

and *Scrobicularia cottardi*. *Hydrobia musaensis* also occurs in freshwaters (Van Damme, 1984).

4.2   The Blue Nile – Lake Tana – Ethiopian Highland

This region, that includes the watershed between the Nile and Awash systems has a malacofauna that stands apart from the rest of the Nile Basin by the occurrence of palaearctic relicts such as *Unio abyssinicus*. This species occurred throughout the Lower Nile during the Holocene but is now confined to Lake Tana (Van Damme, 1984), which is geologically young (Lamb et al., 2007) and harbours no lacustrine endemics. The main distinctive feature of the whole region is the occurrence of a limited number of endemics, namely *Bulinus hexaploidus, B. octoploidus* and *Pisidium ethiopicum*, adapted to montane conditions of small mountain streams and pools above the tree limit. A third important characteristic is the absence of all Afrotropical iridinid bivalves and all Afrotropical prosobranch taxa, except for *Bellamya unicolor* and *Melanoides tuberculata*. This region has hence the lowest species richness within the whole Nile Basin (Tables 1 and 2).

4.3   The Mountain Nile – Sudd – White Nile

The malacofauna of this vast region is appallingly poor, although extensive surface waters, namely the swamps of the Sudd and those north of the Pibor/Sobat Rivers (Machar Marshes) in southern Sudan, are included. Of the 13 gastropod species (Table 1) only one, the bithyniid *Gabbiella schweinfurthi*, may be endemic (Brown et al., 1984; Brown, 1994) and among the 11 bivalve species (Table 2) only the iridinid *Chambardia marnoi* is likely distinctive and confined to this part of the Nile, although further research may prove it to belong to the widespread *C. pfeifferiana* complex (Graf & Cummings, 2007b). The malacofauna of this region is exclusively Afrotropical. It is an impoverished version of the fauna of Lake Chad and shows only a modest relationship to the fauna of the Great Lakes.

4.4   The Great Lakes

The number of species in this region is about twice that of all other parts of the Nile Basin (Tables 1 and 2), due to the high number of endemic species in Lake Albert, Lake Edward and in particular Lake Victoria. However, it remains a pertinent question whether all these putative endemics are specifically distinct. The morphological

differences between the lake-adapted endemics and the fluvio-paludal non-endemics is modest and so is the degree of intralacustrine radiation within each taxon. There actually exists only a single modestly speciose endemic clade among the gastropods of these lakes, namely that of *Bellamya* (Viviparidae) in Lake Victoria, represented by five species. An ongoing molecular investigation (Sengupta et al., 2007) indicates that this supposed 'clade' is not monophyletic, and furthermore that the COI diversity of *Bellamya* within Lake Victoria/L. Albert/L. Kyoga is low (0 to 2.2%), suggesting that either differentiation in *Bellamya* is not accompanied by strong sequence divergences or that the number of *Bellamya* species has been overestimated. Among the bivalves, the only (modestly) speciose clade is that of *Coelatura* in the lakes Victoria, Kyoga, Albert and Edward with four or five species (Graf & Cummings, 2007b) (Fig. 5). Again, it is highly unlikely that this group is monophyletic (Mandahl-Barth, 1988).

The limited diversification in the molluscs of the lakes Albert, Edward, Kyoga and Victoria is in accordance with the geological young age of the lakes (Talbot et al., 2000; Beuning et al., 2002; Goudie, 2005). However, there appears to be an important degree of persistence of this fauna during the Plio-Pleistocene, which contradicts the view that the malacofauna of the Great Lakes mainly consists of lacustrine adapted 'Nilotic' taxa (Mandahl-Barth, 1954, 1988; Scholz & Glaubrecht, 2004). The community in the East African Rift region is partly composed of species, which became taxonomically distinct during the Pliocene. For instance, the unionid species *Coelatura hauttecoeuri* and *Aspatharia divaricata,* presently endemic to Lake Victoria, appear to be no intralacustrine (= that evolved in a lake) endemics, but belong to the Early Pliocene fluvio-paludal fauna of the East African equatorial region. Fossils of these species have been recovered respectively from the Terminal Miocene of the Tugen Hills (De Groeve, 2005) and from Pliocene deposits in the Turkana Basin (Van Bocxlaer pers. data).

Van Damme and Pickford (2003), echoed by Wilson et al. (2004), reached the conclusion that even the spectacular malacofauna of Lake Tanganyika is only in part the result of intralacustrine evolution and that the lake is not primarily a '*living laboratory of evolution*', but rather a refugium for Miocene riverine taxa. Based on the fossil evidence from the Turkana Basin, the same seems to apply to the malacofauna of Lake Victoria, with the important difference that this ~12,000 years old lake may presently act as refugium for taxa of Early Pliocene age instead of Miocene ones (Van Damme pers. data).

The montane fauna of the East African Rift system is extremely poor. Only a single endemic snail has been recorded, the tetraploid *Bulinus membranaceus* in the Aberdare Range and Mau escarpment (Kenya), at altitudes between ~2,000 and 2,800 m (Brown, 1994). In waters on higher altitudes e.g. on Mount Elgon and the Rwenzoris only four pea mussels (*Pisidium casertanum*, *P. armillatum*, *P. invenustum* and *P. montigenum*) occur. *Pisidium invenustum* and *P. montigenum* hardly differ from *P. ovampicum* and may not be distinctive (Mandahl-Barth, 1988). Apparently no palaearctic species, except *P. casertanum*, which is actually a cosmopolitan cold-water species, extend this far south in East Africa.

Fig. 5 The Modern Nile Basin and the distribution of representatives of the genus *Coelatura* Conrad, 1853 exemplifying the separation between the malacofaunas of the Nile north of 5° latitude and the Great Lakes region. (1) *C. aegyptiaca* (Nile, Lake Albert, Omo delta and also in the Chad Basin, Upper Niger and Senegal); (2) *C. bakeri* (Lake Albert); (3) *C. stuhlmanni* (Lake Edward); (4) *C. cridlandi* (Lake Victoria); (5) *C. hauttecoeuri hauttecoeuri* (Lake Victoria); (6) *C. alluaudi* (Lake Victoria); (7) *C. hauttecoeuri kyogae* (Lake Kyoga and the Victoria Nile); (8) *C. rothschildi* (Holocene Lake Turkana, extinct). Molluscs depicted to scale, dashed lines indicate seasonal rivers (wadis), light grey zones indicate swamps

5 Endorheic Basins Formerly Connected to the Nile

Two presently endorheic basin were previously connected with the Nile, namely the Turkana and the Chad Basins. Both connections were temporary and may have occurred repeatedly.

5.1 The Turkana Basin

The claim that a long-lived lake persisted for about 4 million years in the Turkana Basin (Cerling et al., 1979; Williamson, 1981a) has been abandoned, based on stratigraphic, geographic and palaeontological evidence (Brown & Feibel, 1988, 1991; Feibel, 1997, 1999; Van Bocxlaer et al., 2008). During its history the Turkana Basin was predominantly (~85% of the time represented by deposits) occupied by a fluvial Palaeo-Omo system that meandered through the basin and drained in the southeast towards the Indian Ocean (Brown & Feibel, 1991). Between fluvial phases, relatively short lacustrine phases, corresponding to the East African wet phases reported by Trauth et al. (2005), occurred (Brown & Feibel, 1991). Feibel (1997, 1999) recognises the following palaeolakes during Pliocene-Early Pleistocene times: (1) Palaeolake Lonyumun, existing for maximally 100 ka between 4.2 and 4.0 Ma, (2) Palaeolake Lokochot constrained between 3.5 and 3.4 Ma, (3) Palaeolake Lokeridede, existing for ~50 ka around 2.5 Ma, (4) Palaeolake Lorenyang, with a duration of up to 300 ka around 2.0 Ma, (5) Palaeolake Silbo, short-lived and possibly not a single lake but a series of several lakes around 0.9–0.7 Ma. After a long period with structural reorganisation, another palaeolake, here named Palaeolake Bume, formed in Late Pleistocene times, likely during the wet phase of 240–190 ka (MIS 7) or the one at 155–120 ka (MIS 6/5e). The name is derived from the Bume Formation (Lower Omo Basin), where its sediments were recorded (Brown & de Heinzelin, 1983). At present the Turkana Basin is occupied by the endorheic, alkaline Lake Turkana that is the remnant of a larger freshwater lake (~3 times the size of the present Turkana) in terminal Pleistocene-early Holocene times.

Ongoing research shows that the composition of the malacofauna of the Turkana Basin underwent drastic shifts since the Early Pliocene, caused by changes in hydrogeographic connections (Van Bocxlaer et al., 2008; Van Bocxlaer & Van Damme, in press). The sudden morphological shifts observed in the fossil record have originally been presented as *prima facie* fossil evidence for the punctuated equilibrium hypothesis (Williamson, 1981a, 1981b), but the advances in stratigraphy, palaeontology and taxonomy cited above have demonstrated that these pulses reflect invasions rather than bursts of intralacustrine evolution (Van Bocxlaer et al., 2008). This does not imply that no faunal evolution whatsoever was observed in the basin. Some invading fluvial lineages show marked alterations but in comparison with those that yielded the Obwerukan or Tanganyikan thalassoids, these changes remain modest (see Fig. 4). At several stages representatives of the 'Nilotic' community appear in the basin.

There exists no geological evidence for a Plio-Pleistocene connection between the Turkana Basin and the hydrographic basins situated to the north (Nile) and west (Chad), which contained a 'Nilotic' malacofauna (Van Bocxlaer & Van Damme, in press). The intermittent invasion of 'Nilotic' elements in the Turkana Basin suggests that such a link occasionally was established but possibly insufficiently long to leave geomorphological traces (such as the palaeo-Sahabi did).

The dominant Late Pleistocene – Early Holocene molluscan elements in the Turkana Basin are taxonomically related to those presently occurring in Lake Victoria (Cohen, 1981, 1986; Van Bocxlaer & Van Damme, in press). During the hyperarid phase of the terminal Pleistocene, surface water in the Turkana Basin must have been alkaline (Butzer et al., 1969) and in the Lake Victoria Basin only some alkaline pools may have remained (Stager & Day, 2004). Phases when the Turkana Basin held no water have also been recorded during Plio-Pleistocene periods (Brown & Feibel, 1988; 1991; Feibel, 1997, 1999). The geological data and the fossil bearing deposits in the Turkana Basin suggest that freshwater environments of a size suitable to maintain a diverse molluscan community were not or only episodically present. This raises the question where a diversified fauna may have persisted. The best candidate is the area at the base of Mount Elgon, where standing waters persisted during the aridity of the Glacial Maximum (Pickford, pers. comm., 2007).

During the early Holocene a hydrological link was established between Lake Turkana and the Nile, when Lake Turkana spilled into the Lotigipi Plain and the Pibor-Sobat system along its northwestern margin (Butzer et al., 1969; Butzer, 1971; Cohen, 1981). Since the Modern malacofauna of the Sobat-Sudd region differs markedly from the early Holocene Turkana one, there is no evidence that taxa from Turkana migrated northwards via this connection. Alternatively some 'Nilotic' species (e.g. *Coelatura aegyptiaca, Mutela rostrata, M. dubia*) did reach the basin but remained restricted to the fresh waters of Sanderson's Gulf and the Lower Omo (Van Bocxlaer & Van Damme, in press). The lacustrine fauna of Lake Turkana has been severely decimated since the early Holocene, and is at present almost extinct due to the high alkalinity. Based on data from Cohen (1986) and material collected by Frank Brown in 2007, nine species live in the lake proper. Only *Melanoides tuberculata, Gabbiella rosea* and *Ceratophallus kigeziensis* (erroneously identified formerly as *C. natalensis*, see Brown, 1994) are still abundant. Bivalves are absent from the lake, possibly except for a few small populations of *Corbicula fluminalis*. In the fresh water of the Omo delta, a richer fauna, dominated by *Pila wernei* and *Chambardia wahlbergi,* occurs (Tables 1 and 2) (Van Damme, 1976; Van Bocxlaer & Van Damme, in press). Sampling in the Lower Omo remained restricted to occasional surface collecting of larger shells and better sampling will likely yield more species. Additional species, mainly small pulmonates, occur in smaller freshwater ponds around the main lake, e.g., in atapars (springs artificially expanded into cuvettes for watering cattle). In such a standing water we collected *Cleopatra hemmingi* in 2007 and Brown (1994) mentions *Bulinus truncatus and Biomphalaria* sp. from within or near the lake (probably the latter).

5.2   The Chad Basin

The Chad Basin forms a vast expanse in which extensive lakes were formed intermittently at least since the Late Miocene (Goudie, 2005; Griffin, 1999, 2002, 2006). The largest of these was Lake Megachad (Drake & Bristow, 2006). Its existence has been questioned during the 1980s, but SRMT-30 data and Landsat TM imagery have since provided conclusive evidence for a lake around 7,000 BP that was over 173 m deep, with an area of at least 400,000 km^2 (the largest lake may have been ca 837,000 km^2). The overflow of this early Holocene lake was not in the east towards the Nile but in the southwest, towards the Mayo Kébi River and thence westwards to the Atlantic Ocean via the Benué River (Drake & Bristow, 2006).

The fossil malacofauna of the Chad Basin has been poorly studied and the ages of most assemblages are only assumed to be Holocene. However, the arid northern part of the Chad Basin, the Bodélé Depression, undergoes strong wind erosion and it can not be excluded that some assemblages exposed by wind erosion date from the beginning of the Quaternary or earlier. Since the area is now the largest source of atmospheric dust on Earth because of deflation by a powerful north-eastern low-level jet (Washington & Todd, 2005; Koren et al., 2006), the 'Holocene' surface finds may actually consist of fossils and stone artefacts from different time periods concentrated by erosional subsidence as is the case in the Mauritanian desert (Van Damme, 1984). In the few instances where molluscan assemblages are preserved in a stratigraphic context, e.g., at the Falaise d'Angamma (N. Chad), no significant compositional differences can be observed between the Modern community and the Middle Pleistocene one. The oldest Angamma assemblages originally were estimated on the basis of mammalian fauna inference to be of Early to Middle Pleistocene age (Coppens, 1965). This date has since been revised to ~250 ka (Howell, 1978). The Angamma malacofauna is the same as the one in present Lake Chad, indicating that the modern lake fauna did persist during the terminal Pleistocene, even when Lake Chad was dry (Van Damme, 1984).

To date, radar shuttle imagery has not revealed conclusive geophysical evidence indicative for a Chad-Nile connection during Plio-Pleistocene times, although the Holocene Lake Megachad has been suggested to have spilled over towards the east (Beadle, 1981; Leblanc et al., 2006). Since there is no trace of down-cutting at the eastern edge of this vast lake, in contrast with the erosion channel in the southwest (Drake & Bristow, 2006), this Nile-Chad connection apparently was short-lived.

As already stated, the Chad malacofauna is more diversified and archaic than the one of the Nile (see Tables 1 and 2). Endemism in Modern Lake Chad is low and many so-called endemics may not be distinctive (Brown, 1994).

6   Conservation

It is difficult to assess the importance of threats in such an extensive hydrographic system as the Nile Basin. According to recent studies on the Egyptian Nile (Ibrahim et al., 1999; Van Damme pers. data) two main trends can be observed:

(1) the construction of the Aswan Dam and the ensuing reduction of the flow regime of the Egyptian Nile has resulted in a southwards extension to Lake Nasser of species that had formerly been restricted to the Nile Delta.

(2) Palaearctic, boreal species that have been in retreat since the middle Holocene and that were holding out in the Nile Delta have been rapidly disappearing during the last three decades. *Chambardia letourneuxi*, the only endemic bivalve recorded from the Egyptian Nile, has not been collected since the beginning of the twentieth century and probably is extinct. *Unio abyssinicus*, a Palaearctic relict, only surviving in Lake Tana, must be considered as threatened since it is sensitive to climate change. The same may be the case for Ethiopian montane species such as *Bulinus octoploidus* and *Pisidium ethiopicum*. The malacofauna of the White Nile – Mountain Nile and of the Sudd appears not to be threatened. According to Darwall et al. (2005) 25 species of the eastern African region (as defined by IUCN, i.e., including the lakes belonging to the Nile Basin but also L. Malawi and L. Tanganyika) are globally threatened. The main threats are increased sedimentation and habitat loss due to deforestation, drainage of wetlands, and agricultural encroachment. In our opinion, the whole bivalve fauna of Lake Victoria is showing stress. In recent decades, shells of *Coelatura* and *Mutela* appear to have grown significantly larger and thinner, possibly a combined effect of nutrient and temperature increase.

The number of introduced freshwater molluscs in the Nile Basin is low (5–6 species) and none presents an ecological threat. The American ampullariid *Marisa cornuarietis* and the planorbid *Helisoma duryi* were intentionally introduced around 1970 in the Egyptian Nile and Blue Nile, as a biological control agent against *Schistosoma* (Brown, 1994). *Helisoma duryi* is presently recorded from the whole length of the Egyptian Nile (Lofty et al., 2005) but remains relatively uncommon, while *M. cornuarietis* is rare. Another American planorbid, *Biomphalaria glabrata* used in Egypt in *Schistosoma* research, was recorded from the wild in the vicinity of Cairo around 1980 (Brown, 1994). Being an intermediate host of *Schistosoma mansoni,* its escape was considered as a serious public health hazard, but during a recent molecular study of Nile populations the species could not be identified (Lofty et al., 2005). The two other invasive gastropods, the pulmonates *Lymaea columella* and *Physa acuta*, introduced around 1940–50 in the Republic of South Africa probably via the aquarium trade (Appleton, 2003), are presently found all over Africa, including the Nile Basin. However, they do not seem to form an ecological threat, thriving mainly in polluted waters were most autochtonous species have disappeared. There are no known invasive bivalves, though it is possible that some *Corbicula fluminalis* populations in the Lower Nile, being identical to the Levantine morph (Mandahl-Barth, 1988), may be recent arrivals.

References

Adam, W., 1957. Mollusques quaternaires de la région du Lac Edouard. Exploration du Parc National Albert, Mission J. de Heinzelin de Braucourt (1950) 3: 1–171.

Adam, W., 1959. Mollusques pléistocènes de la région du Lac Albert et de la Semliki. Annales du Musée Royal du Congo Belge (Tervuren, Belgique) 25: 1–148.

Appleton, C., 2003. Alien and invasive fresh water Gastropoda in South Africa. African Journal of Aquatic Science 28: 69–81.

Audouin, J. V., 1826. Mollusques de l'Egypte et de Syrie. Explication sommaire des planches dont les dessins ont été fournis par M. J.-C. Savigny, pour l'histoire naturelle de l'ouvrage (offrant un exposé des caractères naturels des genres avec la distinction des espèces). In E. Savigny (ed.), Description de l'Égypte ou Recueil de observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française, publié par les ordres de Sa Majesté l'empereur Napoleon le Grand. Histoire Naturelle, Animaux invertébrés, vol. 1(4): 7–56. E.F. Jomard., Imprimerie imperiale, Paris, 339 pp.

Barash, A. & Z. Danin., 1992. Fauna Palaestina. Mollusca I-Annotated List of Mediterranean Molluscs of Israel and Sinai. Israel Academy of Sciences and Humanities Section of Sciences, Jerusalem, 405 pp.

Beadle, L. C., 1981. The Inland Waters of Tropical Africa: An Introduction to Tropical Limnology. Second Edition. Longman, New York, 475 pp.

Beuning, K. R. M., K. Kelts, J. Russell & B. B. Wolfe, 2002. Reassessment of Lake Victoria – Upper Nile palaeohydrology from oxygen isotope records of lake-sediment cellulose. Geology 30: 559–562.

Bogan, A. E., 1993. Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. American Zoologist 33: 599–609.

Bogan, A. E., 1996. Decline and decimation: the extirpation of unionid bivalves of North America. Journal of Shellfish Research 15: 484.

Böhme, M., 2004. Migration history of air-breathing fishes reveals Neogene atmospheric circulation patterns. Geological Society of America 32: 393–396.

Brown, D. S., 1965. Freshwater gastropod Mollusca from Ethiopia. Bulletin of the British Museum (Natural History), Zoology 12: 37–94.

Brown, D. S., 1980. Freshwater Snails of Africa and Their Medical Importance. Taylor & Francis, London, 487 pp.

Brown, D. S., 1994. Freshwater Snails of Africa and Their Medical Importance. Second revised edition. Taylor & Francis, London, pp. 609.

Brown, F. H. & J. de Heinzelin, 1983. The Lower Omo Basin. In J. de Heinzelin (ed.), The Omo Group. Archives of the International Omo Research Expedition. Annales du Musée Royal de l'Afrique Centrale, Tervuren. Sciences Géologiques 85: 7–24.

Brown, F. H. & C. S. Feibel, 1988. "Robust" Hominids and Plio-Pleistocene Paleogeography of the Turkana Basin, Kenya and Ethiopia. In F. E. Grine (ed.), Evolutionary History of the "Robust" Australopithecines. de Gruyter: New York, 325–341.

Brown, F. H. & C. S. Feibel, 1991. Stratigraphy, depositional environments, and palaeogeography of the Koobi Fora Formation. In J. M. Harris (ed.), Koobi Fora Research Project. Vol. 3. The fossil ungulates: geology, fossil artiodactyls, and palaeoenvironments. Clarendon, Oxford: 1–30.

Brown, D. S., T. Fison, V. R. Southgate & C. A. Wright, 1984. Aquatic snails of the Jonglei region, southern Sudan, and transmission of trematode parasites. Hydrobiologia 110: 247–271.

Butzer, K. W., 1971. The Lower Omo Basin: geology, fauna and hominids of Plio-Pleistocene formations. Naturwissenschaften 58: 7–16.

Butzer, K. W., 1999. Nile Valley, geological evolution. In K. A. Bard (ed.), Encyclopedia of the Archaeology of Ancient Egypt, Routledge, London, pp. 571–573.

Butzer, K. W., F. H. Brown & D. L. Thurber, 1969. Horizontal sediments of the lower Omo Valley: the Kibish Formation. Quaternaria 11: 15–29.

Cailliaud, F., 1826. Voyage à Méroé, au Fleuve blanc, au-delà de Fâzoql dans le midi du Royaume de Sennâr, à Syouah et dans cinq Autres Oasis; fait dans les Années 1819, 1820, 1821 et 1822. Paris, Debure, Tillard, Treuttel & Wurtz.

Campbell, G., C. Jones, A. Lockyer, S. Hughes, D. Brown, L. Noble & D. Rollinson, 2000. Molecular evidence supports an African affinity of the Neotropical freshwater gastropod, *Biomphalaria glabrata* Say 1818, an intermediate host for *Schistosoma mansoni*. Proceedings of the Royal Society of London 267: 2351–2358.

Cerling, T. E., F. H. Brown, B. W. Cerling, G. H. Curtis, & R. E. Drake, 1979. Preliminary correlations between Koobi Fora and Shungura Formations, East Africa. Nature 279: 118–121.

Churcher, C. S., M. R. Kleindienst & H. P. Schwarcz, 1999. Faunal remains from a middle Pleistocene freshwater lake in the Dakhleh Oasis depression, Western Desert, Egypt: palaeoenvironmental reconstructions. Palaeogeography Palaeoclimatology Palaeoecology 154: 301–312.

Cohen, A., 1981. Paleolimnological research at Lake Turkana, Kenya. In J. A. Coetzee & E. M. Van Zinderen Bakker (eds), Palaeoecology of Africa, Routledge, London, 13: 61–82.

Cohen, A., 1986. Distribution and faunal associations of benthic invertebrates at Lake Turkana, Kenya. Hydrobiologia 141: 179–197.

Cohen, A., J. Stone, K. Beuning, L. Park, P. Reinthal, D. Dettman, C. Scholz, T. Johnson, J. King, M. Talbot, E. Brown & S. Ivory, 2007. Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. PNAS 16, 1104: 16422–16427.

Coppens, Y., 1965. Les faunes de Vertébrés quaternaires du Tchad. In Anonymous (ed.), Background to Evolution in Africa. Wenner-Gren Foundation for Antropological Research, University of Chicago Press, Chicago: 89–97.

Cox, L. R., 1926. Fossil Mollusca. In E. J. Wayland (ed.), The Geology and Palaeontology of the Kaiso Bone-Beds. Geological Survey Uganda Department. Occasional Paper 2: 53–71.

Cuttelod, A., M. Seddon, W. Darwall, K. Smith, D. Van Damme, T. Kristensen & C. Lange, 2007. Freshwater mollusc threat assessments in Africa. In K. Jordaens, N. Van Houtte, J. Van Goethem & T. Backeljau (eds), World Congress of Malacology, Antwerp, Belgium 15–20 July 2007. Abstracts: 44.

Daget, J., 1998. Catalogue raisonné des Mollusques bivalves d'eau douce africains. Leiden, Backhuys Publishers and Paris, ORSTOM, 329 pp.

Darwall, W., K. Smith, T. Lowe & J.-C. Vié, 2005. The status and distribution of freshwater biodiversity in Eastern Africa. Occasional Paper of the IUCN species survival commission 31: 1–34.

De Groeve, E., 2005. The Late Cenozoic freshwater molluscs of the Tugen Hills (Kenya): taxonomy, palaeoecology and palaeozoogeography Licentiate dissertation, Palaeontological Research Unit, Ghent University, 121 pp. (in Dutch).

Dohrn, H., 1864. List of shells collected by Capt. Speke during his second journey through Central Africa. Proceedings of the Zoological Society of London, 1865: 116–118.

Drake, N. & C. Bristow, 2006. Shorelines in the Sahara: geomorphological evidence for an enhanced monsoon from palaeolake Megachad. The Holocene 16: 901–911.

Esu, D., 2006. Latest Messinian "Lago-Mare" Lymnocardiinae from Italy: Close relations with the Pontian fauna from the Dacic Basin. Geobios 40: 291–302.

Feibel, C. S., 1997. A terrestrial auxiliary stratotype point and section for the Plio-Pleistocene boundary in the Omo-Turkana Basin, East Africa. Quaternary International 40: 73–79.

Feibel, C. S., 1999. Basin evolution, sedimentary dynamics and hominid habitats in East Africa: an ecosystem approach. In T. Bromage & F. Schrenk (eds), African Biogeography, Climate Change, and Human Evolution. Oxford University Press, Oxford: 276–281.

Fuchs, V. E., 1934. The geological work of the Cambridge Expedition to the East African lakes, 1930–1931. Geological. Magazine 72: 97–122 and 145–166.

Fuchs, V. E., 1936. Extinct Pleistocene Mollusca from Lake Edward, Uganda, and their bearing on the Tanganyika problem. Journal of the Linnean Society of London 40: 93–106.

Gautier, A., 1970. Fossil freshwater Mollusca of the Lake Albert – Lake Edward Rift. Annales du Musée Royal de l'Afrique Central (Tervuren, Belgique) – Sciences Géologiques 67: 1–169.

Genner, M. J., J. A. Todd, E. Michel, D. Erpenbeck, A. Jimoh, D. A. Joyce, A. Piechocki & J. P. Pointier, 2007. Amassing diversity in an ancient lake: evolution of a morphologically diverse parthenogenetic gastropod assemblage in Lake Malawi. Molecular Ecology 16: 517–530.

Germain, L., 1909. Sur les mollusques recueillis dans les anciens monuments Egyptiens. Archives du Muséum d' Histoire Naturel de Lyon 10: 1–15.

Ghamizi, M., 1998. Les mollusques des eaux continentales du Maroc: systématique et bioécologie. Ph. D. thesis, Université Cadi Ayyad, Marrakech, 553 pp.

Glaubrecht, M. & E. E. Strong, 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.

Glaubrecht, M., Z. Feher & T. von Rintelen, 2006. Brooding in *Corbicula madagascariensis* (Bivalvia, Corbiculidae) and the repeated evolution of viviparity in corbiculids. Zoologica Scripta 35: 641–654.

Goren, M., & R. Ortal, 1999. Biogeography, diversity and conservation of the inland fish communities in Israel. Biological Conservation 89: 1–9.

Goudie, A. S., 2005. The drainage of Africa since the Cretaceous. Geomorphology 67: 437–456.

Graf, D. L. & K. S. Cummings, 2006. Freshwater mussels (Mollusca: Bivalvia) of Angola, with the description of a new species, *Mutela wistarmorrisi*. Proceedings of the Academy of Natural Sciences of Philadelphia, 153: 163–194.

Graf, D. L. & K. S. Cummings, 2007a. Zambongo! Freshwater Mussels of the Congo & Zambezi Rivers of Africa. Mussel Project. Philadelphia, 104 pp.

Graf, D. L. & K. S. Cummings, 2007b. Preliminary review of the freshwater mussels (Mollusca: Bivalvia: Unionoida) of northern Africa, with an emphasis on the Nile. Journal of the Egyptian German Society for Zoology 53D: 89–118.

Griffin D. L., 1999. The late Miocene climate of north-eastern Africa: Unravelling the signals in the sedimentary succession. Journal of the Geological Society London 156: 817–826.

Griffin, D. L., 2002. Aridity and humidity: north Africa and the Mediterranean. Palaeogeography Palaeoclimatology Palaeoecology 182: 65–91.

Griffin D. L., 2006. The late Neogene Sahabi rivers of the Sahara and their climatic and environmental implications for the Chad Basin. Journal of the Geological Society 163: 905–921.

Harris, J. M., F. H. Brown & M. G. Leakey, 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. Contributions in Science 399: 1–128.

Heller, J., 2007. A historic biogeography of the aquatic fauna of the Levant. Biological Journal of the Linnean Society 92: 625–639.

Howell, F., 1978. Hominidae. In V. Maglio & H. Cooke (eds), Evolution of African Mammals. Harvard University Press, Cambridge: 154–248.

Huckriede, R. & H. Venzlaff, 1962. Uber eine pluvialseitliche Molluskenfauna aus Kordofan (Sudan). Paläontologisch Zeitschrift, H. Schmidt-Festband, Stuttgart: 93–109.

Ibrahim, A. M., H. M. Bishai & M. T. Khalil, 1999. Freshwater molluscs of Egypt. Egyptian Environmental Affairs Agency, National Biodiversity Unit (10).

Issawi, B. & J. F. McCauley, 1992. The Cenozoic rivers of Egypt: the Nile problem. In B. Adams & R. Friedman (eds), The Followers of Horus. Oxbow Press, Oxford: 1–18.

Jorgensen, A., K. T. Kristensen & H. Madsen, 2008. A molecular phylogeny of apple snails (Gastropoda, Caenogastropoda, Ampullariidae) with an emphasis on African species. Zoologica Scripta 37: 245–252.

Koren, I., Y. J. Kaufman, R. Washington, M. C. Todd, Y. Rudich, J. V. Martins & D. Rosenfeld, 2006. The Bodélé depression: a single spot in the Sahara provides most of the mineral dust to the Amazon Forest. Environmental Research Letters 1, doi:10.1088/1748–9326/1/1/014005.

Korniushin, A. V. & M. Glaubrecht, 2006. Anatomy and reproduction of viviparous *Pisidium* (*Parapisidium*) *reticulatum* Kuiper, 1966: Implications for the phylogeny of Sphaeriidae (Mollusca: Bivalvia: Heterodonta). Organisms, Diversity and Evolution 6: 185–195.

Krijgsman, W., F. J. Hilgen, L. Raffi, F. J. Sierro & O. S. Wilson, 1999. Chronology, causes and progression of the Messinian salinity crisis. Nature 400: 652–655.

Lamb, H. F., C. R. Bates, P. V. Coombes, M. H. Marshall, M. Umer, S. J. Davies & E. Dejen, 2007. Late Pleistocene desiccation of Lake Tana, the source of the Blue Nile. Quaternary Science Reviews 26: 287–299.

Leakey, M. G. & J. M. Harris (eds), 2003. Lothagam: the dawn of humanity in Eastern Africa. Columbia University Press: New York.

Leblanc, M., C. Leduc, F. Stagnitti, P. J. Van Oevelen, C. Jones & L. A. Major, 2006. Evidence for Megalake Chad, north-central Africa, during the Late Quaternary from satellite data. Palaeogeography Palaeoclimatology Palaeoecology 230: 230–242.

Leloup, E., 1950. Lamellibranches. Résultats Scientifiques de l'Exploration Hydrobiologique du Lac Tanganyika (1946–1947). Institut Royal des Sciences Naturelles Belge 3(1): 1–153.

Lihoreau, F., J-R. Boisserie, L. Viriot, Y. Coppens, A. Likius, H. T. Mackaye, P. Tafforeau, P. Vignaud & M. Brunet, 2006. Anthrocothere dental anatomy reveals a late Miocene Chado-Libyan bioprovince. Proceedings of the National Academy of Sciences 103: 8763–8767.

Lofty, W., R. Dejong, A. Abdel-Kader & E. Loker, 2005. A molecular survey of *Biomphalaria* in Egypt: is *B. glabrata* present? American Journal of Tropical Medicine and Hygiene 73: 131–139.

Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D.G. Herbert, R. Hershler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong & F. G. Thompson, 2004. The Global Decline of Nonmarine Mollusks. Bioscience 54: 321–330.

Magyar, I. & O. Sztanó, 2007. Terminal Miocene Events in the Pannonian Basin. Joannea-Geologie und Paläontologie 9: 55–57.

Mandahl-Barth, G., 1954. The freshwater mollusks of Uganda and adjacent territories. Annales du Musée Royal du Congo Belge, Sciences Zoologiques 32: 1–206.

Mandahl-Barth, G., 1988. Studies on African freshwater bivalves. In K. Kristensen & E. Svenningsen (eds), Danish Bilharziasis Laboratory, Charlottenlund, Denmark: 1–161.

Martens, K.,1997. Speciation in ancient lakes. Trends in Ecology and Evolution 12: 177–182.

McCauley, J. F., G. G. Schaber, C. S Breed, M. J. Grolier, C. V. Haynes, B. Issawi, B. C. Elachi & R. Blom, 1982. Subsurface valleys and geoarchaeology of the eastern Sahara revealed by shuttle radar. Science 218: 1004–1020.

Moore, J., 1903. The Tanganyika Problem. London, Hurst & Blackett.

Morgan, J. A. T., R. J. DeJong, Y. Jung, K. Khallaayoune, S. Kock, G. M. Mkoji & E.S. Loker, 2002. A phylogeny of planorbid snails, with implications for the evolution of *Schistosoma* parasites. Molecular Phylogenetics and Evolution 25: 477–488.

Morris, P. J., 1995. Phylogenetic analysis of endemic viviparids in the Pliocene of the Edward-Mobutu Rift, Uganda-Zaire. Comptes Rendus de l'Academie des Sciences, Paris, serie IIa 320: 447–453.

Murray, A., 2006. A new channid (Teleostei: Channiformes) from the Eocene and Oligocene of Egypt. Journal of Paleontology 80: 1172–1178.

Olivier G.-A., 1801–1807. Voyage dans l'Empire Othoman, l'Égypte et la Perse, fait par ordre du gouvernement pendant les six premières années de la République. Paris, H. Agasse, 3 volumes.

Park, J. K. & Ó Foighil, D., 2000. Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. Molecular Phylogenetics and Evolution 14: 75–88.

Pickford, M., 1986. Cainozoic Palaeontological Sites of Western Kenya. Müncher Geowissenschaftliche Abhandlungen (A) Geologie und Paläontologie 8: 1–151.

Pickford, M., B. Senut & D. Hadoto, 1993. Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. I: Geology. Centre International pour la formation et les échanges géologiques (CIFEG), Orleans, Occasional Publications 24: 1–190.

Pilsbry, H. & J. Bequaert, 1927. The Aquatic Molluscs of the Belgian Congo. Bulletin of the American Museum of Natural History 53: 69–602.

Redfield, T. F., W. H. Wheeler & M. Often, 2003. A kinematic model for the development of the Afar Depression and its palaeogeographic implications. Earth and Planetary Science Letters 216: 383–398.

Ricciardi, A. & J. B. Rasmussen, 1999. Extinction rates of North American Freshwater Fauna. Conservation Biology 13: 1220–1222.

Rossiter, A. & H. Kawanabe (eds), 2000. Biology of Ancient Lakes: Biodiversity, Ecology and Evolution. Advances in Ecological Research 31. Academic, London.

Said, R., 1981. The Geological Evolution of the Nile River. Springer Verlag, New York.

Said, R., 1993. The River Nile. Geology, Hydrology and Utilisation. Pergamon, Oxford.

Salama, R. B., 1987. The evolution of the River Nile. The buried saline rift lakes in Sudan. Journal of African Sciences 6: 899–913.

Salama, R. B., 1997. Rift basins of Sudan. In R. C. Selley (ed.) African Basins. Sedimentary Basins of the World 3: 115–149. Elsevier. Amsterdam.

Salama, R. B., 2005. The evolution of the River Nile in Sudan. http://www.managedwater.com

Schattner, U., Z. M. Ben-Avraham, M. Reshef, G. Bar-Am & M. Lazar, 2006. Oligocene–Miocene formation of the Haifa basin: Qishon–Sirhan rifting coeval with the Red Sea–Suez rift system Tectonophysics 419: 1–12.

Scholz, H., & M. Glaubrecht, 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.

Sengupta, M., T. Kristensen, H. Madsen & A. Jørgensen, 2007. Molecular diversity and phylogenetic relationships of the family Viviparidae (Gastropoda, Mollusca) with special emphasis on the *Bellamya* radiations in the Rift Valley Lakes of Africa. In K. Jordaens, N. Van Houtte, J. Van Goethem & T. Backeljau (eds), World Congress of Malacology, Antwerp, Belgium 15–20 July 2007. Abstracts: 202–203.

Sivan, N., J. Heller & D. Van Damme, 2006. Fossil Viviparidae (Mollusca: Gastropoda) of the Levant. Journal of Conchology 39: 207–219.

Smith, J. R., R. Giegengack & H. P. Schwarcz, 2004. Constraints on Pleistocene pluvial climates through stable-isotope analysis of fossil-spring tufas and associated gastropods. Palaeogeography Palaeoclimatology Palaeoecology 206: 157–175.

Smith, J. R., A. L. Hawkins, Y. Asmeron, V. Polyak & R. Giegengack, 2007. New age constraints on the Middle Stone Age occupations of Kharga Oasis, Western Desert, Egypt. Journal of Human Evolution 52: 690–701.

Spamer, E. E. & A. E. Bogan, 1993. New records of mollusca for Grand Canyon National Park and Arizona. The Southwestern Naturalist 38: 293–298.

Stager, J. C. & J. J. Day, 2004. Comment on 'Origin of the superflock of cichlid fishes from Lake Victoria, East Africa'. Science 304: 963.

Stewart, K., 2001. The freshwater fish of Neogene Africa (Miocene–Pleistocene): systematics and biogeography. Fish and Fisheries 2: 177–230.

Szabo, B. J., C. V. Haynes & T. A. Maxwell, 1995. Ages of Quaternary pluvial episodes determined by uranium-series and radiocarbon datings of lacustrine deposits of eastern Sahara. Palaeogeography Palaeoclimatology Palaeoecology 113: 227–242.

Talbot, M. R., M. A. Williams & D. A. Adamson, 2000. Strontium isotope evidence for a Late Pleistocene reestablishment of an integrated Nile drainage network. Geology 28: 343–346.

Thieme, M. L., R. Abell, M. L. J. Stiassny, P. Skelton, B. Lehner, G. G. Teugels, E. Dinerstein, A. Kamden Toham, N. Burgess & D. Olson, 2005. Freshwater ecoregions of Africa and Madagascar: A conservation assessment. Island Press, Washington, London, 431 pp.

Trauth, M. H., M. A. Maslin, A. Deino & M. R. Strecker, 2005. Late Cenozoic moisture history of East Africa. Science 309: 2051–2053.

Van Bocxlaer, B., D. Van Damme & C. Feibel, 2008. Gradual versus punctuated equilibrium evolution in the Turkana basin molluscs: evolutionary events or biological invasions? Evolution 62: 511–520.

Van Bocxlaer, B. & D. Van Damme (in press). The fossil malacofauna of the Turkana Basin: Iridinidae Swainson, 1840 and Etheriidae Deshayes, 1830 (Bivalvia: Etheroidea). Journal of Systematic Palaeontology. DOI: 10.1017/514 77201908002587.

Van Damme, D., 1976. Systematics, ecology and evolution of the fossil freshwater molluscs of the Lake Rudolf Basin (Ethiopia, Kenya). Ph. D. thesis, Ghent University, 310 pp (in Dutch).

Van Damme, D., 1984. The Freshwater Mollusca of Northern Africa: Distribution, Biogeography and Palaeoecology. In H. J. Dumont (ed.), Developments in Hydrobiology 25: 1–164. The Hague, Junk.

Van Damme, D. & M. Pickford, 1994. The Late Cenozoic Freshwater Molluscs of the Albertine Rift, Uganda-Zaire: Evolutionary and Palaeoecological Implications. In B. Senut & M. Pickford (eds), Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. II: Palaeobiology. Centre International pour la formation et les échanges géologiques (CIFEG), Orleans, Occasional Publications 29: 71–87.

Van Damme, D. & M. Pickford, 1995. The late Cenozoic Ampullariidae (Mollusca, Gastropoda) of the Albertine Rift Valley (Uganda-Zaire). Hydrobiologia 316: 1–32.

Van Damme, D. & M. Pickford, 1999. The late Cenozoic Viviparidae (Mollusca, Gastropoda) of the Albertine Rift Valley (Uganda-Congo). Hydrobiologia 390: 171–217.

Van Damme, D. & M. Pickford, 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.

Van Damme, D., M. Ghamizi, G. N. Soliman & A. McIvor (in prep). IUCN-list of the freshwater molluscs of northern Africa. IUCN-Med.

Van Neer, W., 1994. Cenozoic fish fossils from the Albertine Rift Valley in Uganda. In B. Senut & M. Pickford (eds), Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. II: Palaeobiology. Centre International pour la formation et les échanges géologiques (CIFEG), Orleans, Occasional Publications 29: 89–124.

Verheyen, E., W. Salzburger, J. Snoecks & A. Meyer, 2003. Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. Science 300: 325–329.

Verheyen, E., W. Salzburger, J. Snoecks & A. Meyer, 2004. Response to 'Comment on origin of the superflock of cichlid fishes from Lake Victoria, East Africa. Science 304: 963.

Vermeij, G. J., 1987. Evolution and escalation: An ecological history of life. Princeton/N.Y. Princeton University Press.

von Martens, E., 1886. Subfossile Süsswasser-Conchylien aus Aegypten. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin: 120–126.

Washington, R. & M. C. Todd, 2005. Atmospheric controls on mineral dust emission from the Bodélé Depression, Chad: Intraseasonal to interannual variability and the role of the low level jet. Geophysical Research Letters 32: L17701 10.1029/2005GL023597.

Wesselingh, F. P., G. C. Cadée & W. Renema, 1999. Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. Geologie & Mijnbouw 78: 165–174.

West, K., A. Cohen & M. Baron, 1991. Morphology and behaviour of crabs and gastropods from Lake Tanganyika: Implications for lacustrine predator-prey coevolution. Evolution 45: 589–607.

West, K. & A. Cohen, 1994. Predator-crab coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. Archiv für Hydrobiologie, Beiheft. Ergebenisse in Limnologie 44: 267–283.

West, K. & E. Michel, 2000. The Dynamics of Endemic Diversification: Molecular Phylogeny Suggests an Explosive Origin of the Thiarid Gastropods of Lake Tanganyika. In Rossiter, A. & H. Kawanabe (eds), Ancient Lakes: Biodiversity, Ecology and Evolution. Advances in Ecological Research. 31: 331–354. Academic Press, San Diego.

West, K., E. Michel, J. A. Todd, D. Brown & J. Clabaugh, 2003. The gastropods of L. Tanganyika. Diagnostic keys, classification and notes on the fauna. Occasional publications. International Association of Limnology, London, 130 pp.

Williams, M. A. J., D. Adamson, M. Talbot & P. Aharon, 2001. Quaternary lakes, palaeochannels and dunes in the White Nile Valley. In F. Gasse et al. (eds), Past climate variability through Europe and Africa. Atlas conferences, Aix en Provence, France, Augustus 27–31, 2001. Abstract.

Williams, M. A. J., D. Adamson, J. R. Prescott & F. M. Williams, 2003. New light on the age of the White Nile. Geology 11: 1001–1004.

Williamson, P. G., 1981a. Palaeontological documentation of speciation in Cenozoic molluscs from the Turkana Basin. Nature 293: 437–443.

Williamson, P. G., 1981b. Morphological stasis and developmental constraints. Real problems for neo-Darwinism. Nature 294: 214–215.

Williamson, P. G., 1985. Evidence for an early Plio-Pleistocene rainforest expansion in East-Africa. Nature 315: 487–489.

Williamson, P. G., 1990. Late Cenozoic mollusc faunas from the north western African Rift (Uganda-Zaire). Virginia Museum of Natural History Memoirs 1: 125–139.

Wilson, A. B., M. Glaubrecht & A. Meyer, 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. Proceedings of the Royal Society of London, Biological Sciences 271: 529–536.