

Modern and early Holocene mollusc fauna of the Ounianga lakes (northern Chad): implications for the palaeohydrology of the central Sahara



BERT VAN BOCXLAER,^{1,2*} DIRK VERSCHUREN,² GEORG SCHETTLER³ and STEFAN KRÖPELIN⁴

¹Research Unit Palaeontology, Department of Geology and Soil Science, Ghent University, Krijgslaan 281-S8, B-9000 Ghent, Belgium

²Limnology Unit, Department of Biology, Ghent University, Ghent, Belgium

³GeoForschungsZentrum Potsdam, Potsdam, Germany

⁴African Archaeology Unit, Institute of Prehistoric Archaeology, University of Cologne, Köln, Germany

Received 28 April 2010; Revised 20 October 2010; Accepted 22 October 2010

ABSTRACT: The fresh and saline lakes of Ounianga Kebir and Serir in northeastern Chad are among the very few permanent aquatic ecosystems currently existing in the hyper-arid core of the Sahara desert. The confirmed modern fauna of aquatic molluscs at Ounianga comprises three widespread species (*Melanoides tuberculata*, *Biomphalaria pfeifferi* and *Lymnaea natalensis*), of which only the first appears to maintain a thriving population. We recovered seven more species of gastropods, among which one is new to science (*Gabbiella ouniangaensis*), and one bivalve species from early Holocene outcrops of diatomaceous limestone at Ounianga Serir. All species except one are known to be commonly spread between lake and river systems by birds, and in its entirety this species-rich fossil mollusc fauna of Ounianga Serir resembles that of other Saharan lake sites known to have been hydrologically isolated during the early Holocene. The impoverished modern mollusc fauna, which lacks even the widespread and opportunistic species *Bulinus truncatus*, may have become established relatively recently through new colonisation events, following eradication of the early Holocene mollusc fauna during a later episode of high salinity or desiccation. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: freshwater molluscs; palaeoclimatology; zoochory; biogeography; green Sahara; African Humid Period.

Introduction

The drying of the early Holocene ‘green Sahara’ (Claussen and Gaylor, 1997) to the world’s largest warm desert today is one of the most prominent Holocene environmental changes worldwide. The mid Holocene aridification of the Sahara is widely believed to have occurred abruptly around 5500 years ago, based on the deep-sea record of terrigenous dust deposition in the eastern tropical Atlantic Ocean (deMenocal *et al.*, 2000). However, multiple-proxy evidence preserved in the uniquely continuous and well-resolved sediment record of Lake Yoa at Ounianga in northeastern Chad (19–20° N, 20–21° E) now suggests a more gradual drying of the terrestrial ecosystem, at least in the east-central Sahara (Kröpelin *et al.*, 2008). Lake Yoa and other lakes at Ounianga (Fig. 1) are among the very few permanent aquatic ecosystems currently existing in the arid core of the Sahara desert, where rainfall is erratic and annual evaporation can exceed 6000 mm (Kröpelin, 2007). These lakes thus present a unique opportunity to study the Holocene evolution of aquatic environments in the Sahara in response to climate drying (Eggermont *et al.*, 2008). The Ounianga lakes are maintained against today’s extreme moisture deficit by inflow of fossil groundwater from a large sandstone aquifer that was last recharged during the early Holocene (Hissene, 1986). Owing to variation among lakes in the balance of subsurface inflow, subsurface outflow, lake volume and the evaporating lake surface, the modern system comprises a wide range of fresh to hypersaline (electrical conductivity ranges from 230 to 157 000 $\mu\text{S cm}^{-1}$) aquatic environments. In the early Holocene, the Ounianga lakes were much deeper and covered a larger area, as testified by lacustrine limestone outcrops at Ounianga Serir up to ~80 m above the current lake surface (George and Kröpelin, 2000; Kröpelin, 2007, provides a digital elevation model of the early Holocene Ounianga Serir). At that time, standing surface waters were abundant in North Africa, so

that the Ounianga lakes were certainly not as isolated as they currently are (Hoelzmann *et al.*, 2004), but the nature and stability of the hydrological connectivity of Ounianga Kebir and Serir to the central Chad Basin with Lake Mega-Chad remain poorly known. Recently, Grenier *et al.* (2009) combined SRTM digital elevation data of the Ounianga region with a climatic water-balance model to reach the preliminary conclusion that the early Holocene Ounianga Kebir was at least periodically connected to downstream Lake Mega-Chad via surface outflow. Another important question is whether the relatively extensive modern-day freshwater ecosystems at Ounianga Serir have existed continuously since the early Holocene ‘African Humid Period’ and hence may be inhabited by relict faunas that formerly had a much wider distribution in the central Sahara. Lake Yoa at Ounianga Kebir is certain to have never desiccated in the last 6000 a (Kröpelin *et al.*, 2008) but evolved from fresh to hypersaline between 4200 and 3800 a ago, forcing freshwater aquatic organisms to retreat to relatively marginal habitat in a small, partly isolated creek fed by fresh groundwater inflow.

A field survey of the modern aquatic mollusc fauna at Ounianga Serir and Kebir in 2004 combined with exploratory sampling of mollusc-bearing early Holocene limestone outcrops at Ounianga Serir in 1999 and 2004 created the opportunity for a first faunal comparison. Early Holocene mollusc fauna have been reported from many Saharan localities (e.g. Germain, 1935; Gautier, 1980; Rosso, 1983; Van Damme, 1984; Pachur and Altmann, 2006), including the larger Ounianga region (Llabador, 1962, Mollusques subfossiles du Nord-Tchad collectionnées lors des missions paléontologiques (1960–1961) par Yves Coppens, 1968 - unpublished), however, often with the purpose of constructing a palaeoenvironmental context to archaeological studies. Lacking adequate illustrations or morphological descriptions, species identifications in most of these studies are unverifiable, unless the original material can be re-examined. Here we perform a detailed taxonomic and morphological comparison of the early Holocene and modern mollusc fauna of the Ounianga lakes,

*Correspondence: B. Van Bocxlaer, as above.
E-mail: bert.vanbocxlaer@ugent.be

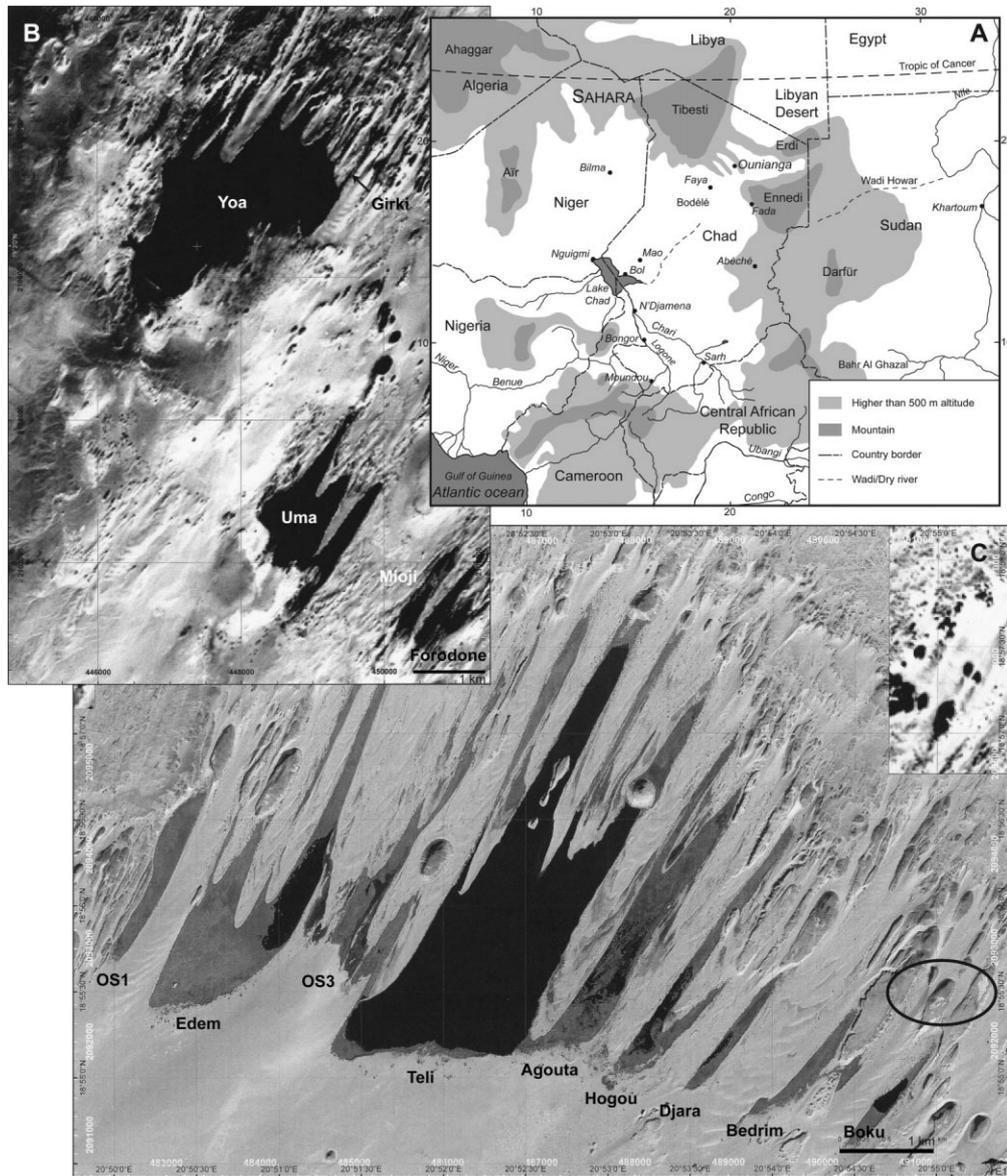


Figure 1. Map of central North Africa (A) with Ounianga located in northeastern Chad between the Tibesti and Ennedi mountain ranges, and satellite images of the two lake clusters Ounianga Kebir (B) and Ounianga Serir (C). At Ounianga Kebir all lakes are hypersaline, except the fresh Girki spring creek entering Lake Yoa from the northeast. At Ounianga Serir the central Lake Teli is hypersaline, all other lakes are fresh to slightly saline and partly or fully covered by floating aquatic vegetation (dark grey). The location of sampled early Holocene limestone outcrops near Lake Boku is indicated by a ellipse. The black scale bars on the satellite images (bottom right) represent 1 km.

and use information on the biology, ecology and dispersal capacity of recovered species to reconstruct aspects of the Holocene palaeoenvironment at Ounianga that relate to the above questions on the palaeohydrology of the east-central Sahara.

Study area

The Ounianga lakes are situated just south of the Erdi Plateau between the Tibesti and Ennedi mountains, clustered in two lake districts about 50 km apart (Fig. 1b and c): Ounianga Kebir (19° 02' N, 20° 31' E) and Ounianga Serir (18° 56' N, 20° 52' E). The lakes occupy Pleistocene deflation basins at the foot of an E–W oriented escarpment of the Mesozoic Nubian Sandstone Complex (Hissene, 1986; Wolff, 1964) constituting the northeastern rim of the Chad Basin. The topography of the Ounianga region is a relic of late Tertiary fluvial erosion at the outlet of Neogene Lake Chad, overprinted by aeolian processes during the Quaternary, when the Sahara was predominantly dry

(Griffin, 2006; Castañeda *et al.*, 2009). Ravines dissecting the escarpment channel strong trade winds from the northeast, resulting in the accumulation of sand dunes below the escarpment's cliff face. Over time, these dunes have gradually encroached upon the lake basins (Fig. 1b and c).

Ounianga Kebir consists of four hypersaline lakes, of which Lake Yoa (~4 km²) is the largest (Table 1). Dunes along its northeastern shore partially enclose Girki, a freshwater creek fed by abundant groundwater inflow (Fig. 1b). At Ounianga Serir, dunes extend across the basin, creating a series of seven elongated fresh and saline lakes (Edem, Teli, Agouta, Hogou, Djara, Bedrim and Boku) and two reed-covered depressions (OS1, OS3; Fig. 1c) arranged parallel to the main prevailing wind direction. The hypersaline Lake Teli (~10 km²) is the largest natural lake in the Sahara (Pesce, 1968); Lake Edem (~2 km²) is to our knowledge the largest permanent freshwater lake. With surface elevations of ~344 m (Teli at Ounianga Serir) and ~379 m (Yoa at Ounianga Kebir) the lakes lie ~60–100 m above the current water level of Lake

Table 1. Summary of lake morphology, water and bottom-substrate data of permanent waters at Ounianga Kebir and Ounianga Serir, measured in October 2004.

Lake		Surface (km ²)	Depth (m)	Cond. ($\mu\text{S cm}^{-1}$)	Surf. T (°C)	O ₂ (mg L ⁻¹)	Ca (mg L ⁻¹)*	Mg (mg L ⁻¹)*	DIC (mg L ⁻¹)*	pH	Bottom substrate
Ounianga Kebir											
OK1	Yoa	5.1	26.5	64 700	21.3	0.06	1.23	6.7	2 940	10.0	Sandy mud
Spring	Girki	0.0001	1.8	269	22.9	5.38	19.5	8.1	21.2	7.3	Sand, plant debris
OK2	Uma	1.7	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
OK3	Mioji	0.5	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
OK4	Forodone	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Ounianga Serir											
OS1	n.a.	0.4	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
OS2	Edem	2.0	6.8	621	24.1	6.42	37.1	31.8	86.2	7.7	Calcareous mud
OS3 [†]	n.a.	0.6	0.2	920	23.8	3.72	n.a.	n.a.	n.a.	7.4	Mud on sandstone
OS4	Teli	6.5	5.0	157 000	25.4	4.96	1.76	71.1	4 789	8.6	Calcareous mud
OS5	Agouta	1.3	3.6	2 680	26.4	5.21	67.6	60.3	105	7.6	Calcareous organic mud
OS6	Hogou	0.6	4.6	1 900	22.8	6.05	63.8	61.9	94.3	7.7	Calcareous mud
OS7	Djara	0.2	8.0	1 320	23.6	4.15	85.0	43.9	88.7	7.5	Calcareous mud
OS8	Bedrim	0.3	0.4	788	20.4	4.38	86.8	19.1	62.1	7.0	Plant debris
OS9	Boku	0.2	13.0	329	23.1	7.15	44.6	6.4	25.5	7.5	Coarse sand

Surface area includes water covered by floating vegetation; depth reflects maximum depth in open water. *Calcium, magnesium and dissolved inorganic carbon (DIC) concentrations in the hypersaline lakes Yoa and Teli are expressed as mg kg⁻¹ brine. Lakes are indicated both with their fieldwork codes and (if available) their official name. n.a., not available. [†]Measurements for OS3 were made on its outflow.

Chad. Ounianga is located ~300 km beyond the normal reach of summer monsoon rainfall from the south, and wintertime rainfall originating from the Mediterranean only occasionally reaches the Tibesti massif ~400 km to the northwest (Kröpelin *et al.*, 2008). The region currently experiences a hyperarid (<5 mm annual rainfall) subtropical climate with distinct temperature seasonality; monthly mean temperatures range from 26 to 42 °C during the day, and from 15 to 26 °C at night (weather data courtesy of the Direction des Ressources en Eau et de la Météorologie, N'Djaména, Chad). Consequently, also the water temperature of the Ounianga lakes shows considerable seasonal variation. In late October 2004, open water surface temperature varied between 21 and 27 °C among the lakes (Table 1). Surface-water temperature was low in wind-exposed larger lakes due to evaporative cooling, in relatively deep lakes (e.g. Boku) and in shaded waters (e.g. Girki and Bedrim). It was highest in small, sunny lakes where a rather complete reed fringe shelters against wind stress, and in Lake Teli where elevated brine density limits wind-driven mixing. Maximum summertime water temperatures are unknown, but likely exceed 30 °C in the shallow lakes largely covered by *Phragmites*, such as Djara and Bedrim. The water column of the deeper lakes exhibits thermal stratification. Temperature and oxygen profiles surveyed in mid January 1999, early December 2003 and late October 2004, together with the subtropical location, suggest a monomictic regime with one mixing and one stratification phase annually. Deep-water temperatures of the stratified lakes (Boku, Yoa) indicate that the wintertime minimum surface-water temperature is ~14–17 °C.

As mentioned, the Ounianga lakes can currently persist by virtue of subsurface inflow of fresh groundwater from a large fossil aquifer, which compensates for strong lake surface evaporation. This aquifer was last recharged during the early Holocene, probably in part by infiltration of precipitation in the Tibesti mountains to the northwest (Maley, 2000), and in the Kufra Basin to the northeast (Brinkmann *et al.*, 1987). The vast Nubian Sandstone aquifer, which feeds the Ounianga lakes, extends to northern Sudan and to the Western Desert of Egypt (Hesse *et al.*, 1987; Edmunds *et al.*, 2004).

The presence of permanent freshwater lakes in the middle of the Sahara desert appears paradoxical, as strong evaporation is expected to increase salinity. In Ounianga Kebir, standing freshwater habitat is limited to the Girki creek and small freshwater springs, partly isolated from the hypersaline Lake Yoa by dune tongues and/or shoreline vegetation. The lake system of Ounianga Serir, however, comprises a natural 'evaporation pump' (George and Kröpelin, 2000; Kröpelin, 2007), in which the sand dunes extending across the basin (Fig. 1c) function as dams behind which fresh water rising from the surrounding aquifer can accumulate without being mixed with saline water. The pump's engine is the large and central Lake Teli, a large evaporation plane that creates a hydrological gradient by which water is drawn from the peripheral lakes through the dunes separating them. This constant flow removes dissolved salts from the peripheral lakes and accumulates them in Lake Teli. The decreasing ratio of fresh groundwater input to lake surface evaporation between each pair of adjacent lakes results in a conductivity gradient from the basin's periphery towards Lake Teli (Table 1). All lakes except Teli are sufficiently fresh (up to 2900 $\mu\text{S cm}^{-1}$) for floating mats of reed (*Phragmites australis*) to develop; these mats cover the lake surface partly (e.g. Edem) or almost completely (Bedrim), further reducing evaporation.

Dominant species of emergent aquatic vegetation, besides *Phragmites australis*, are *Cyperus laevigatus* and *Typha australis*. Submerged macrophyte beds are locally well developed in the more transparent lakes, including *Utricularia* and *Ceratophyllum* in Lake Bedrim, *Chara* in Lake Edem, and *Potamogeton* in Lake Boku and in the Girki spring creek. The slightly brackish lakes Hogou and Agouta lack submerged vegetation, despite adequate transparency (Secchi depth was 3.95 and 2.95 m, respectively, in October 2004). Bottom substrates are highly variable, ranging from coarse sand containing little organic matter in Lake Boku and sandy mud with coarse organic detritus in Girki, to fine-grained carbonate muds with moderate (Edem, Djara) to high (Hogou, Agouta) organic matter content. At all lakes, date palm leaves hanging in the water provide additional habitat for periphyton and associated invertebrate communities. Small cichlid fishes (*Hemichromis letourneuxi* and *Sarotherodon galilaeus borkuanus*) (Trewavas and Teugels, 1991; J. Snoeks, Royal

Table 2. Results of accelerator mass spectrometric radiocarbon dating on bulk carbonate from six limestone samples from Ounianga Serir, in stratigraphic sequence from bottom to top: radiocarbon age with standard error, the corresponding 2σ calendar age intervals (both in a BP) and the relative area under the distribution curve corresponding to the 2σ envelopes.

Sample	Lab code	^{14}C age	95.4% (2σ) cal. age range	Area
Y91-2	GX-26791	8900 ± 110	9 656–10 240	0.99
Y70-6B	GX-25722	8800 ± 120	9 555–10 174	1.00
Y70-8T	GX-25723	7880 ± 110	8 455–9 000	1.00
Y88-4	GX-26792	7790 ± 230	8 169–9 266	1.00
Y91-1	GX-25724	7700 ± 110	8 301–8 777	0.98
Y91-1	GX-26790	7620 ± 70	8 320–8 583	1.00

Museum of Central Africa, Tervuren, pers. comm. 2005) occur in lakes Djara, Boku, the Girki creek at Lake Yoa and quite possibly also in the other freshwater Ounianga lakes.

Material and methods

This study concerns collections of living molluscs currently inhabiting the Ounianga lakes, and of fossil molluscs extracted from outcropping deposits of early Holocene diatomaceous limestone to the NNE of Lake Boku (Fig. 1c). Six ^{14}C dates on bulk carbonate sediment from these primary deposits yielded early Holocene ages (Table 2); calibrations were performed with Calib v. 5.1 (Stuiver and Reimer, 1993) using the IntCal04 calibration curve (Reimer *et al.*, 2004). Smaller remnants of laterally correlated deposits also occur nearby Lake Teli, but were not included in the present study.

The modern aquatic mollusc fauna of the Ounianga lakes was sampled by visually screening emergent aquatic vegetation and shallow-water sediments, and by dragging a hand-net (100 μm mesh) through submerged vegetation. Living mollusc specimens were preserved in 70% ethanol. Temperature, pH, dissolved oxygen and conductivity (specific conductance at 25 °C, in $\mu\text{S cm}^{-1}$) were measured in the field with a Hydrolab

Quanta CTD profiler. Samples for analysis of water chemistry were collected and processed following standard methods (see Eggermont *et al.*, 2007, for details). Here we limit discussion to data on the biologically active elements calcium and magnesium.

Fossil molluscs were obtained from 11 limestone samples collected in 1999 (sample codes with 'Y' in Table 3) and 2004 (with 'YY'). All samples except two *ex situ* surface-picked samples (Y55-SP and Y70-SP) were sieved through mesh sizes of 2 mm and 710 μm to separate a coarse fraction with large mollusc specimens and fragments of limestone matrix from the fine fraction containing specimens of small species and juvenile shells. The matrix was disintegrated in H_2O by stirring, gentle ultrasonic treatment and limited mechanical fractionation by hand. A small number of shells may have remained inside fragments of concreted matrix after this treatment; these were excluded from further analysis. From the fine fraction only adult specimens of small-sized species and opercula were included in the quantitative analyses. The quality of mollusc preservation was similar in all samples and generally very good, as even the most fragile species yielded intact shells. This is indicative for deposition in a low-energy environment and, given the high ratio of determinable shells versus shell debris, abundances are reported as specimen counts.

Photographs were taken at optical magnifications of 8–40 \times using a Leica Wild M10 binocular fitted with an Olympus DC 50 digital camera. Measurements were made with Image Tool 3.00 (Wilcox *et al.*, 2002) on the acquired digital images, and verified with Vernier calliper measurements. Dimensions are given in mm as total height (H) by total width (B), sometimes supplemented by aperture height (h) and aperture width (b). Fossil finds dated to the Late Pleistocene–early Holocene in older literature (e.g. Van Damme, 1984) refer to deposits with ages considered to fall within the ca. 15 000–5500 cal a BP period.

Results

The early Holocene lake deposits at Ounianga Serir contain 11 species of aquatic molluscs: 10 gastropods and one heterodont bivalve (Table 3). Three gastropod species belong to the gill-

Table 3. Analysed samples of early Holocene limestone at Ounianga Serir, indicating the amount of sediment screened and the number of adult specimens recovered of each mollusc species present.

Sample code	Sample code (and dry weight)											
	YY48-1 (75 g)	YY49-3 (63.9 g)	YY54-1 (84 g)	YY56-1 (61.3 g)	YY62-5 (102.5 g)	YY67-1 (61.4 g)	Y55-SP (n.a.)	Y70-SP (n.a.)	Y70-3 (51 g)	Y70-6 (64.4 g)	Y90-2 (34.5 g)	Total (598 g)
Gastropoda Caenogastropoda												
<i>Gabbiella ouniangaensis</i>	0	26	6	6	23	2	0	22	12	0	54	151
<i>Melanooides tuberculata</i>	35	3	5	0	10	3	0	19	20	19	56	170
<i>Cleopatra bulimoides</i>	0	1*	0	0	1*	0	0	0	0	0	0	2
Gastropoda Heterobranchia												
<i>Valvata nilotica</i>	38	9	96	15	18	38	0	45	20	0	184	463
<i>Lymnaea natalensis</i>	41	29	23	6	17	16	1	41	55	15	64	308
<i>Afrogyrus coretus</i>	0	(p)	(p)	(p)	(p)	(p)	0	4	(p)	6	(p)	10
<i>Cyraululus costulatus</i>	17	2	2	0	4	1	0	0	0	(p)	10	36
<i>Biomphalaria pfeifferi</i>	115	79	96	32	64	95	6	77	168	39	195	966
<i>Bulinus truncatus</i>	23	10	25	6	4	11	1	14	48	18	36	196
<i>Lentorbis junodi</i>	0	0	0	0	(2)	0	0	0	0	0	0	(2)
Bivalvia Heterodonta												
<i>Pisidium ovampicum</i>	0 (p)	0 (p)	244 (p)	0	16 (p)	0	0	0	0	0	0 (p)	260
Total	269	159	497	65	159	166	8	222	323	97	599	2564

Samples with 'Y-' and 'YY-' codes were obtained in 1999 and 2004, respectively. Y55-SP and Y70-SP are *ex situ* surface-picked samples and were not weighed (n.a.) or sieved. Counts of adult specimens normally include only material from the large sieved fraction (>2 mm); (p) indicates that a species was found only in the fine-sieved fraction (0.710 mm $< x < 2$ mm) of a sample, as juveniles; since adults of *Lentorbis junodi* were found exclusively in the fine fraction, these were also counted. *Material reworked from older deposits.

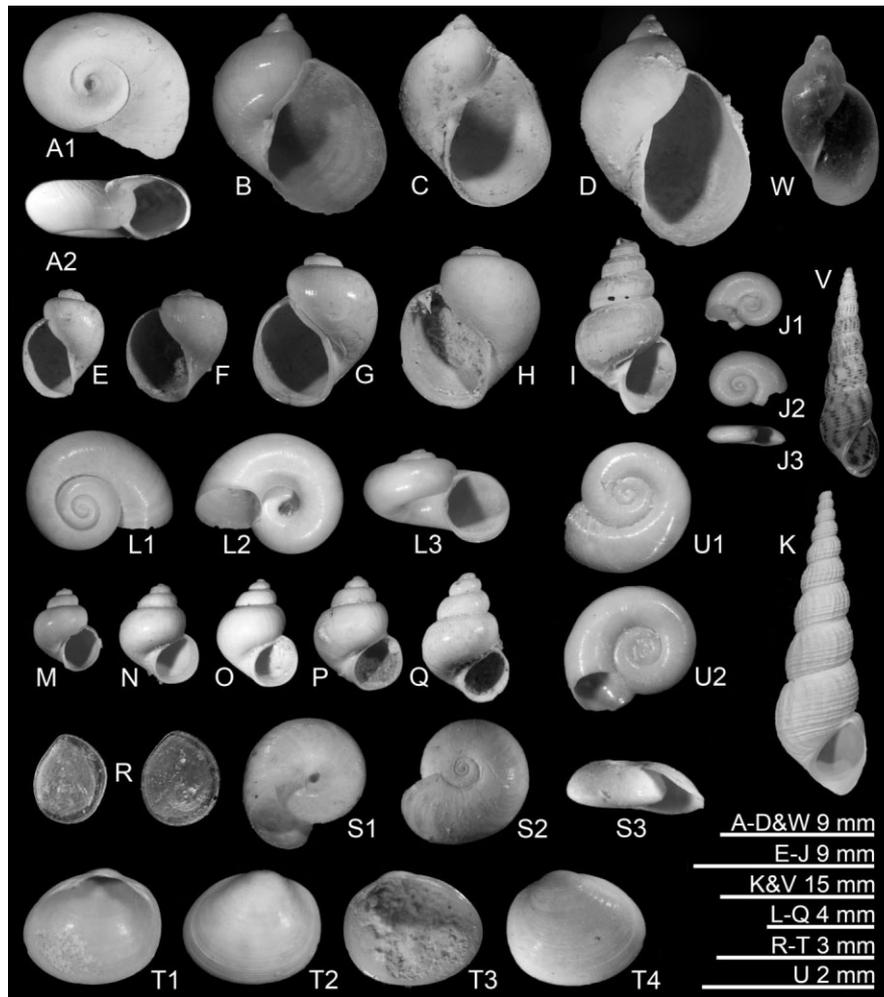


Figure 2. Early Holocene (A–U) and modern (V–W) aquatic molluscs from Ounianga. A, *Biomphalaria pfeifferi* (YY67-1); B–D, *Lymnaea natalensis* (B: Y70-6; C, D: Y70-SP); E–H, *Bulinus truncatus* (E, G: YY48-1 Base; F: Y70-3; H: Y90-2); I, *Cleopatra bulimoides* (YY62-5 Top); J, *Gyraulus costulatus* (YY54-1 Base); K, *Melanooides tuberculata* (Y70-SP); L, *Valvata nilotica* (YY67-1); M–Q, *Gabbiella ouiangaensis* (M: YY49-3; N–P: YY90-2; Q: Y90-1); R, opercula of *G. ouiangaensis* (left: Y70-3; right: YY49-3); S, *Lentorbis junodi* (YY62-5); T, *Pisidium ovampicum* (YY54-1 Base; T1 and T4 left valve, T2 and T3 right valve); U, *Afrogyrus coretus* (YY54-1 Base); V, *Melanooides tuberculata*; W, *Lymnaea natalensis*.

breathing Caenogastropoda; the other seven are Heterobranchia – *Valvata* is a basal Heterobranchia and the other six are lung-breathing Pulmonata (Bouchet *et al.*, 2005). Three of the gastropods, namely *Melanooides tuberculata*, *Lymnaea natalensis* and *Biomphalaria pfeifferi*, comprise the known modern freshwater mollusc fauna at Ounianga.

Taxonomy: differential species diagnoses

Gastropoda Caenogastropoda

Gabbiella ouiangaensis sp. nov. Van Bocxlaer. Fig. 2: M (holotype), N, O (paratypes), P, Q, R (opercula); Fig. 3 (operculum).

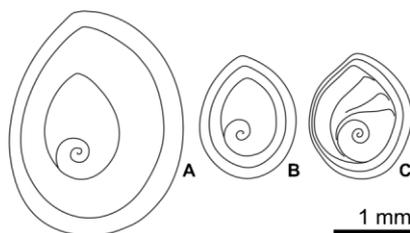


Figure 3. Operculum of *G. ouiangaensis* sp. nov. (C) compared with those of *G. tchadiensis* (A) and *G. senaariensis* (B); the latter two are redrawn from Mandahl-Barth (1968).

Medium-sized *Gabbiella* species (Table 4) with conical globose shell; spire variable but usually equal to or slightly higher than the apertural height. About four inflated, evenly convex whorls are separated by deep sutures. Sculpture consisting of very fine growth lines only. Aperture round to oval; columellar margin not reflected, parietal edge reflected over the previous whorl, outer margin evenly and regularly curved. Umbilicus open, sometimes leading to a basal subsutural groove. Operculum (Fig. 3C) ovate, similar in

Table 4. Dimensions of early Holocene *Gabbiella ouiangaensis* shells and opercula from Ounianga.

	H	B	h	b
Shells				
YY49-3 (type; Fig. 2M)	3.14	2.52	1.55	1.28
YY90-2 (paratype; Fig. 2N)	3.78	2.97	1.69	1.58
YY90-2 (paratype; Fig. 2O)	4.08	3.05	1.78	1.52
YY90-2 (Fig. 2P)	4.33	3.33	1.95	1.72
Y90-1 (Fig. 2Q)	4.89	3.30	1.86	1.58
Opercula				
Y70-3 (Fig. 2R, left)	1.69	1.37	–	–
YY49-3 (Fig. 2R, right)	1.74	1.41	–	–

H, total height; B, total width; h, apertural height and b, apertural width (in mm).

size to that of *G. tchadiensis* Mandahl-Barth, 1968, but more angular at the top and with a considerably larger, slightly eccentric spiral part.

Gabbiella ouiangaensis sp. nov. morphologically resembles *G. tchadiensis*, *G. senaariensis* (Küster, 1852) and to lesser extent *G. schweinfurthi* (Jickeli, 1874). It is distinguished from *G. tchadiensis* by its wide open umbilicus. Some specimens possess an unusually high spire, similar to that of the much larger *G. senaariensis*. The operculum is taxonomically diagnostic in *Gabbiella* (Mandahl-Barth, 1968; Van Damme, 1984) and that of *G. ouiangaensis* is distinct from all three above-mentioned species. It differs from that of *G. tchadiensis* (Fig. 3A) by its relatively larger width, its extra whorl in the central spiral area and the basal attachment of the inner, spiral part to the outer, concentric part. Moreover, the spiral growth lines are incurved, which is not the case in *G. tchadiensis* or *G. senaariensis*. The latter species (Fig. 3B) has a much larger operculum with a relatively smaller, but more elongated spiral area, attached to the concentric part at the columellar side. The operculum of the less resembling *G. schweinfurthi* (not shown) also has few whorls in the central spiral area, a lateral attachment and smaller size.

Gabbiella ouiangaensis is present and moderately common in most of the early Holocene samples from Ounianga (Table 3). Its biology and ecology are unknown but, comparable to the extant *G. tchadiensis*, it probably lived on aquatic vegetation. Possibly it has become extinct.

Melanoides tuberculata (O. F. Müller, 1774). Fig. 2: K (fossil), V (modern).

Fossil shells conical and slender with spiral height $>3\times$ the apertural height. Usually 10 (up to 12) regularly increasing, inflated whorls with well-rounded periphery; shoulder present but weak; sutures distinctive. Surface sculpture with growth lines and sinusoidal rows of weakly pronounced nodules; the sub-sutural row of nodules is inconspicuous. Aperture oval at the base and acute at the top; outer apertural margin smoothly curved along the growth lines; umbilicus closed. Modern *M. tuberculata* from Lake Boku are similar in size, but generally more slender in shape (Fig. 2, V vs. K; Table 5).

Melanoides tuberculata occurs in almost any type of flowing and standing fresh water in warm temperate to tropical climates (Brown, 1994), but ephemeral pools are suboptimal (Van Damme, 1984). It prefers a sandy or silty bottom (Lévêque *et al.*, 1983), living endobenthically during the day and feeding at night on benthic microalgae, fine detritus, epiphytic algae and decaying plants (Madsen, 1992). It reproduces predominantly asexually, disperses easily and is resistant to a wide

variety of environmental stress (Brown, 1994; Samadi *et al.*, 1999; Facon *et al.*, 2003). *M. tuberculata* is distributed throughout Africa and southern Asia, and is an exotic invader to America. In tropical Africa it is widespread, but appears to be lacking from large parts of humid West Africa and the Congo Basin, and in arid northern Africa (Algeria, Libya, Chad) only isolated populations occur (Brown, 1994). However, in the Late Pleistocene and early Holocene it was common throughout the present-day Sahara (Van Damme, 1984). We recovered *M. tuberculata* from most early Holocene samples, with a mean abundance of $\sim 7\%$ (Table 3). One sample of *ex situ* surface-picked fossils contains seven large specimens (31–34 mm). Llabador (unpublished 1968) reported more surface finds of this species in the larger Ounianga region, together with fragments of the endobenthic bivalve *Corbicula fluminalis*, but the origin and age of this presumably lost material are uncertain. The only living population of *M. tuberculata* at Ounianga occurs in Lake Boku, where 26 living specimens were collected from hundreds of specimens observed crawling at densities on the order of $\sim 50\text{ m}^{-2}$ on sandy substrate between *Phragmites* shoots. Two of these living specimens are relatively large (23–24 mm); the others are smaller (Table 5). The reported adult size range for this species is 30–36 mm (Thompson, 1984); however, its maximum size is poorly known because the sterilising effect of parasitic trematode flukes causes gigantism (Ben-Ami and Heller, 2005; Genner *et al.*, 2008), with individuals growing to 47 mm (Brown, 1994; Van Damme, 1984).

Cleopatra bulimoides (Olivier, 1804). Fig. 2I.

Shell thick-walled and conical, spiral height $\sim 2\times$ that of the aperture. About 5 whorls, with angulated upper whorls and more evenly curved, weakly shouldered lower whorls. Surface sculpture consisting of growth lines only but traces of two dark-brown bands are present. Aperture acute-ovate; outer lip evenly curved; parietal part of the inner lip reflected over the previous whorl, columellar part curved and slightly reflected. Umbilicus open. The only full-grown fossil shell recovered measures 9.0×5.1 mm, which is within the reported range (typical form 16×9 mm; slender form 22×9 mm; Van Damme, 1984; Brown, 1994).

This species has a predominantly epibenthic lifestyle on various substrates in stagnant and slow-flowing waters (Brown, 1994). At present it occurs in Egypt, Sudan, Ethiopia and Kenya, with a westward extension to southern Chad, Senegal and Gambia (Brown, 1994). Late Pleistocene to early Holocene populations are also known from Niger, Mali and Libya (Van Damme, 1984). We found only two *C. bulimoides* specimens in the early Holocene material from Ounianga. In contrast to all other fossil material, the shells are abraded and corroded, suggesting that they had been reworked from older lake deposits. We dated one specimen directly, which confirmed its early Holocene age (Beta-273033; 95.4% (2σ) calibrated age range: 7620–7480 cal. a BP).

Gastropoda Heterobranchia

Valvata nilotica Jickeli, 1874. Fig. 2: L1–L3.

Shell discoid to ovate; not as high-spired as the modern Ethiopian subspecies *V. n. scioana* Pollonera, 1888, spiral height $<1/2$ the aperture height. About $2\frac{1}{4}$ rapidly increasing whorls with rounded periphery; umbilicus wide open. Shell sculpture consisting of fine growth lines only. Aperture round to ovate, sometimes angular at the base; columellar side of the aperture not reflected; apertural plane forming an angle with the columellar axis. Early Holocene specimens from Ounianga are mostly within the size range of modern populations

Table 5. Dimensions of early Holocene and modern *M. tuberculata* shells from Ounianga.

Shells	H	B	H/B ratio
Y70-SP-M1 (Fig. 2K)	34.2	10.2	3.35
Y70-SP-M2	31.3	10.0	3.13
Y90-2-M3	16.1	5.2	3.10
YY54-1-M4	11.8	4.6	2.57
YY62-5-M5	12.5	4.5	2.78
ModernB-01	23.3	7.4	3.15
ModernB-02	24.2	8.9	2.72
ModernB-03 (Fig. 2V)	18.6	5.1	3.65
ModernB-04	12.7	3.7	3.43
ModernB-05	16.4	4.7	3.49

H, total height; and B, total width (in mm).

Table 6. Dimensions in mm of early Holocene and modern *L. natalensis* shells from Ounianga.

Shells	<i>H</i>	<i>B</i>	<i>h</i>	<i>b</i>
Y70-6 (Fig. 2B)	12.0	9.1	8.9	6.0
Y70-SP (Fig. 2C)	11.5	7.9	8.9	5.2
Y70-SP (Fig. 2D)	13.9	8.9	10.2	5.4
YY54-1-L2	10.7	6.8	7.6	4.4
Modern G-01 (Fig. 2W)	10.3	6.3	7.0	3.8

H, total height; *B*, total width; *h*, aperture height; *b*, aperture width (all in mm).

($H \times B = 3.3 \times 5.0$ mm; Brown, 1994), but some are distinctly larger (up to 3.55×5.51 mm).

Valvata nilotica inhabits lakes, permanent pools and slow-flowing streams, preferably with dense aquatic vegetation (Brown, 1994). All species of the genus *Valvata* are hermaphroditic, and produce gelatinous egg clusters (Zhadin, 1965). The current distribution of *V. nilotica* is limited to northern Egypt, northern Sudan and the Ethiopian highlands (Brown, 1994), but during the early Holocene it occurred further west in Chad, Libya and Algeria; and further southeast in southern Ethiopia, northern Kenya and Somalia (Van Damme, 1984). *V. nilotica* is abundant in the early Holocene Ounianga material (Table 3).

Lymnaea (Radix) natalensis Krauss, 1848. Fig. 2: B–D (fossil), W (modern).

Shell elongated to ovate; spiral height $< 1/2$ the aperture height. About $4\frac{1}{4}$ weakly shouldered whorls. Sculpture consisting of distinct growth lines. Aperture large to very large with an oval base and angular top; outer lip evenly curved, parietal part of the inner lip reflected over the previous whorl, columellar part straight or reflected. Umbilicus open. Modern *L. natalensis* shells are highly variable in shape, and measure up to 25.0×14.5 mm but are often smaller (Van Damme, 1984; Brown, 1994). The modern shells from Ounianga morphologically resemble the fossil material but are smaller and more slender (Fig. 2 and Table 6). However, the five modern individuals available comprise too small a sample for reliable statistical comparison.

Lymnaea natalensis inhabits permanent streams, artificial impoundments, shallow-water seeps and (rarely) seasonal ponds (Brown, 1994; Utzinger and Tanner, 2000). It is less tolerant to desiccation than *Biomphalaria pfeifferi* (Cridland, 1967; see below), but can still survive drought for several months at least (Bitakaramire, 1968). It prefers plant detritus as substrate (Utzinger and Tanner, 2000), and may be favoured by moderate organic pollution (Brown, 1994). At Ounianga, we found living specimens on decaying palm leaves in the Girki creek (16 specimens, mostly immature), and on decaying reed in Lake Djara (one immature specimen). *L. natalensis* is widespread in sub-Saharan Africa, with northernmost populations occurring in the southern Sahel zone of Sudan, Chad, Mali, Senegal and Gambia; only in the Nile basin does it occur further north (Brown, 1994). During the Late Pleistocene and early Holocene, it occurred throughout the Sahara and Sahel (Van Damme, 1984). It is common in all studied early Holocene samples from Ounianga (Table 3). In addition, many more small (juveniles) to medium-sized specimens were present, a characteristic also typical of thriving modern *L. natalensis* populations, when compared to other pulmonate species (Utzinger and Tanner, 2000).

Africanogyrus coretus (de Blainville, 1826). Fig. 2: U1–U2.

Shell discoid, very small and extremely thin-walled. About $2\frac{3}{4}$ planispiral whorls that rapidly increase in size, which is rather atypical for this species; periphery convex, sometimes angulated. Sculpture consists of marked growth lines. Aperture with curved outer lip; inner lip fairly straight; apertural plane weakly to distinctly oblique. Umbilicus wide. Fossil Ounianga specimens are considerably smaller than the dimensions presented by Brown (1994) for modern adults (0.7×2.5 to 1.2×5.0 mm): the photographed, most probably adult specimen measures 0.34×1.60 mm. Morphologically the material resembles specimens of dwarfed modern populations from Kharga and Dakhla Oasis in Egypt (Van Damme, 1984).

Africanogyrus coretus typically inhabits permanent waters but has also been recovered from flood waters of the Nile, ditches, rainpools and small spring pools (Brown *et al.*, 1984). It prefers habitats rich in aquatic vegetation (Brown, 1994), where it often occurs on the underside of floating lily leaves and among leaf litter (Brown, 1994). Modern *A. coretus* is probably widespread throughout Africa (Brown, 1994); North African populations are reported from Libya, Egypt, Sudan and Mauritania (Brown and Mandahl-Barth, 1973; Brown *et al.*, 1984). During the Late Pleistocene and early Holocene period it also occurred at various sites in Chad and Algeria (Van Damme, 1984). This species was found in virtually all fossil samples, but mostly as juveniles; adults are rare ($< 1\%$ of the total count; Table 3).

The former generic name *Afrogyrus* Brown and Mandahl-Barth is a junior homonym and has been replaced (Özdikmen and Darilmaz, 2007).

Gyraulus costulatus (Krauss, 1848). Fig. 2: J1–J3.

Shell discoid, small and thin-walled. About 3 planispiral whorls rapidly increasing in size; periphery bluntly angular. Surface sculpture consisting of regularly spaced, moderately pronounced ribs, growth lines and a weak carina somewhat below the centre of the periphery. Aperture broad and triangular to ovate. Umbilicus wide. Brown (1994) gives maximum dimensions of 1.5×6.6 mm; the figured specimen measures 1.1×3.5 mm.

Gyraulus costulatus occurs in all kinds of permanent surface waters rich in vegetation (Brown, 1994). It is commonly distributed throughout tropical Africa, and its northern range is determined by isolated populations in southeastern Algeria, Libya and Egypt (Brown, 1994). Late Pleistocene–early Holocene populations are also known from various other North African countries, including Chad (Van Damme, 1984). At Ounianga we found fossil specimens in several samples but in low abundance (Table 3).

Lentorbis junodi (Connolly, 1922). Fig. 2: S1–S3.

Shells small, fragile and thin-walled; discoid and lens-shaped with convex upper side and flattened basal side. About $3\frac{1}{2}$ whorls; periphery angulated, body whorl large, largely enveloping the penultimate whorl; lamellae (septa) present or absent – if present they are faintly visible only on the basal side. Shell sculpture consists of growth lines. Aperture with angulated outer lip; inner lip reflected over previous whorls. Umbilicus narrow. Maximum reported size is 2.0×5.5 mm (Brown, 1994). The two fossil specimens from Ounianga are about half this size (1.11×2.71 and 1.02×2.60 mm), still within the known adult size range.

Lentorbis junodi is difficult to distinguish from *Segmentorbis angustus* (Jickeli, 1874) without reference to soft-part anatomy because the number of lamellae – the only diagnostic feature on

the shell – is regularly ambiguous (Brown, 1994; Girod, 1998). We attribute our well-preserved material to *Lentorbis junodi*, because one of the shells has no lamellae and those of the other shell are faint.

Lentorbis junodi occurs in Lake Chad, Ethiopia, southern Sudan and throughout eastern Africa (Brown, 1994), but is rare even in its optimal habitat of aquatic vegetation in marshes, slow-flowing rivers and streams (Brown *et al.*, 1984). This is the first reported finding of a fossil *Lentorbis*.

Biomphalaria pfeifferi (Krauss, 1848). Fig. 2: A1–A2 (fossil); the single modern specimen is not depicted.

Comparatively large discoid snails, shell diameter $>2.5\times$ its height. $3\frac{1}{2}$ whorls with inflated, well-rounded apical sides, bluntly angular basal sides; periphery well rounded. Surface sculpture consists of distinct growth lines. Aperture ovate, outer lip oblique. Umbilicus wide. Fossil Ounianga shells measure up to 4.11×9.73 mm, which is distinctly smaller than average modern specimens (5.2×13.0 mm; Brown, 1994).

Biomphalaria pfeifferi occurs in a wide range of surface waters including lakes, streams, irrigation channels, reservoirs and some seasonal aquatic habitats, but not in extensive papyrus swamp (Brown, 1994). It prefers shallow substrates of plant detritus or rocks close to shore (Uttinger and Tanner, 2000). After desiccation of all surface water, *B. pfeifferi* can survive several months in wet mud or other favourable microhabitats, and even exposed to sun and wind with soil surface temperatures of 45°C it can survive for up to 30 days (Cridland, 1967). *B. pfeifferi* is widely distributed across tropical Africa, and in northern Africa known from isolated populations in southeastern Algeria, Niger, Chad, and southwestern Arabia (Brown, 1994). It was widespread in the present Sahara during the Late Pleistocene and early Holocene period, and is the only *Biomphalaria* species found in Quaternary deposits within the Chad Basin (Van Damme, 1984). It is the most abundant mollusc in the early Holocene assemblages of Ounianga Serir, occurring in all samples and accounting for $\sim 38\%$ of all adult specimens (Table 3). Also one subadult or dwarfed adult was found living in Lake Boku.

Bulinus truncatus (Audouin, 1827). Fig. 2: E–H.

Shell sinistral, ovate or globose, shell walls of medium thickness and with variable spiral height (usually $\sim 1/3$ of the apertural height). About $2\frac{3}{4}$, moderately shouldered whorls; body whorl rapidly increasing in size. Surface sculpture consisting of fine growth lines. Aperture ovate, with evenly curved outer lip; inner lip with parietal part reflected over previous whorls, columellar part slightly concave or straight, not projected nor – or only slightly – reflected. Early Holocene shells from Ounianga are up to 8.27×6.28 mm in size, within the modern size range (Brown, 1994).

Bulinus truncatus occurs in both flowing and standing perennial waters, and in seasonally drying ponds, but not in the ephemeral pools frequented by *B. senegalensis* and *B. tropicus* (Brown, 1994). Compared to *Biomphalaria pfeifferi*, *B. truncatus* has a greater tolerance to fluctuating chemical and thermal conditions (Appleton, 1978) and is able to withstand drought for up to 10 months, provided that the drying occurs gradually (McCullough, 1962). This species is a highly successful disperser, often rapidly colonising man-made reservoirs in remote locations. At present the main distribution of *B. truncatus* in northern Africa is in the Maghreb region, northern Egypt, Sudan and westward across the Sahel to Mauritania (Brown, 1994). Its northern limit is situated in Portugal, the Mediterranean islands and the Near East, and its southern limit in DR Congo and Malawi (Brown, 1994). During

the Late Pleistocene and early Holocene the species was widespread in currently arid North Africa and Arabia (Van Damme, 1984). We found it in all studied fossil samples, but it was less abundant than *Lymnaea natalensis* and *Biomphalaria pfeifferi* (Table 3).

Bivalvia Heterodonta

Pisidium ovampicum Ancey, 1890. Fig. 2: T1–T4.

Shell fragile, oval and moderately inflated. Beaks low, located at or slightly posterior to the valve midline, not protruding above the dorsal margin. Anterior, posterior and ventral margin regularly curved; dorsal margin gently curved. Surface sculpture consisting of very fine, concentric growth lines. Hinge plate very narrow with narrow, straight teeth. Two cardinal teeth in the left valve, one in the right; both anterior and posterior lateral teeth unpaired in the left valve, paired in the right valve. The largest Ounianga specimens (3 mm) fit the reported adult size of modern specimens (Mandahl-Barth, 1988).

Pisidium ovampicum lives in small lakes, ponds and rivers and is currently distributed in East Africa and Madagascar (Mandahl-Barth, 1988). In equatorial countries such as Uganda and Kenya it is found in the relatively cold waters of tropical mountain ranges (Rwenzori, Mt Elgon and Mt Kenya; Mandahl-Barth 1988), suggesting a relatively low temperature optimum. Late Pleistocene–early Holocene finds in the present Sahara are known from Falaise d'Angamma in Chad and the Trou au Natron in Libya (Böttcher *et al.*, 1972; Van Damme 1984). *Pisidium* shells account for $\sim 10\%$ of the adult fossil molluscs in the Ounianga material.

Discussion

The species richness of the early Holocene mollusc fauna indicates that a stable aquatic ecosystem with great habitat diversity existed at Ounianga Serir. The large size and depth of the early Holocene lake, as inferred from the location and elevation of mollusc-bearing deposits (Kröpelin, 2007), probably buffered its aquatic habitats against seasonal variation in water balance, physical and chemical conditions. The spatial freshwater habitat heterogeneity was likely higher compared to the situation today, since the reed mat cover must have been substantially smaller, allowing diverse submerged and emergent vegetation to develop. In sharp contrast to this species-rich early Holocene fauna stands the current, impoverished fauna. In the following, we discuss environmental factors that may influence the composition of the modern mollusc fauna at Ounianga, namely (i) geological and climate-related abiotic habitat characteristics, and (ii) substrate composition and aquatic vegetation. Although predation is a potentially important factor as well, no molluscivore animals are known to inhabit Ounianga today or in the past. Subsequently, we place the composition of the early Holocene fauna in a wider geographical and palaeohydrological context, to infer the origin of the modern fauna.

Environmental controls on the modern mollusc fauna of Ounianga

The principal physical and chemical aspects of aquatic mollusc habitat are salinity, pH, calcium concentration, oxygen supply, temperature and substrate composition (Brown, 1994). Salinity, the concentration of dissolved minerals, is a major determinant of aquatic invertebrate community structure (e.g. Wollheim and Lovvorn, 1995), either directly through the osmotic stress of high solute concentrations (Bayly, 1972), or indirectly via its effect on the occurrence of important habitat provided by salt-

sensitive aquatic vascular plants (Verschuren *et al.*, 2000). For most freshwater organisms, including molluscs, the optimal salinity range varies between electrical conductance values of 70 and 700 $\mu\text{S cm}^{-1}$ (Beadle, 1981; Hammer, 1986). Values exceeding 1100–1600 $\mu\text{S cm}^{-1}$ progressively eliminate molluscs. The few gastropods surviving in waters with conductivity values above 4200 $\mu\text{S cm}^{-1}$ often consist of little more than the chitinous periostracum (Van Damme, 1984; Brown, 1994) due to a shortage of dissolved calcium. At Ounianga, living snails were found to occur in the relatively dilute waters of Girki creek (230–270 $\mu\text{S cm}^{-1}$; *L. natalensis*), L. Boku (330 $\mu\text{S cm}^{-1}$; *M. tuberculata* and a single juvenile *B. pfeifferi*) and in L. Djara (1320 $\mu\text{S cm}^{-1}$; a single juvenile *L. natalensis*). We found no living snails in L. Edem (620 $\mu\text{S cm}^{-1}$) or Bedrim (790 $\mu\text{S cm}^{-1}$), despite apparently favourable water chemistry. The salt-tolerant species *Biomphalaria pfeifferi* and *Bulinus truncatus* (Grébillat and Gaston, 1975), reported from Tunisia in waters with conductivities of 1220–2440 $\mu\text{S cm}^{-1}$ at 18°C (Meier-Brook *et al.*, 1987), are currently rare or absent at Ounianga, whereas the more salt-sensitive *L. natalensis* (Meier-Brook *et al.*, 1987) is present even in L. Djara. This suggests that salinity is not the main determinant of modern mollusc occurrences at Ounianga. All the freshwater lakes, i.e. all surveyed lakes except Teli and Yoa, also have pH values (7.0–7.70) optimal for molluscs (Williams, 1970; Brown, 1994).

Williams (1970) classified aquatic mollusc habitat on the basis of dissolved calcium (Ca) and CaCO_3 concentrations as soft (0–5 mg L^{-1} Ca, <20 mg L^{-1} CaCO_3), intermediate (5–40 mg L^{-1} Ca, 20–200 mg L^{-1} CaCO_3) or hard (>40 mg L^{-1} Ca, >200 mg L^{-1} CaCO_3). At Ounianga, regional groundwater (19.2 mg L^{-1} Ca in a well at Ounianga Serir) and that of the Girki creek (18.4 mg L^{-1} Ca) have an intermediate hardness; all other Ounianga waters are harder (35–83 mg L^{-1} Ca; see Table 1). Among the snail species currently living at Ounianga, *B. pfeifferi* and *L. natalensis* occur in waters of all types, but prefer hard over soft waters (Schutte and Frank, 1964). Hence Ca availability by itself does not allow explaining the observed pattern of mollusc occurrence at Ounianga. The calcium depletion that often occurs in evaporating waters due to chemical precipitation and burial of CaCO_3 (e.g. Gorham *et al.*, 1983) can be prevented by high Mg concentrations, because of the inhibitory effect of Mg on calcite precipitation. However, Meier-Brook *et al.* (1987) investigated freshwater mollusc distribution in relation to the Ca/Mg ratio and found no correlation within the studied range of values (0.63–3.40). In the freshwater lakes at Ounianga, Ca/Mg ratios vary between 1.03 (Hogou) and 6.97 (Boku), but no relation is apparent with the lakes where living molluscs were found.

The Ounianga lakes undergo substantial seasonal temperature fluctuation. Ambient temperature influences both the survival and reproduction of adult molluscs and the growth of juveniles (Brown, 1994), but assessing its impact on field populations is difficult because molluscs can migrate towards favourable microhabitats (Shiff, 1966). Laboratory tests showed adult *B. pfeifferi* to have a relatively wide optimal temperature range of 20–29°C, while juveniles have a more confined optimum of 23–24°C (De Kock and Van Eeden, 1981; Appleton and Eriksson, 1984). Populations of this and other tropical snails are extinguished within a month from waters with constant high temperatures (>34°C), but continuous exposure to such temperatures is probably extreme even for Ounianga because of the day–night fluctuations, wind-induced cooling and inflow of cool fossil groundwater. Wintertime surface temperatures (14–17°C) are suboptimal for tropical species but also appear insufficiently harsh to extinguish them. The impact of high water temperature on freshwater organisms is often indirect, by

reducing oxygen solubility and enhancing its consumption by bacterial decomposition of organic matter. Respiration by dense algal blooms at night can also lead to intermittent oxygen depletion. Dissolved oxygen concentrations below 2.5 mg L^{-1} have adverse effects on freshwater fauna (Donnelly and Appleton, 1985). Pulmonate snails are better adapted to a temporary oxygen shortage than caenogastropods (Brown, 1994). Oxygen supply seems adequate in all fresh Ounianga lakes today, with daytime surface concentrations ranging from 3.3 to 6.8 mg L^{-1} in open water and among submerged vegetation; seasonal fluctuations and changes at the transition between the stratified and mixed stage are not documented, however.

Among the species comprising the modern mollusc fauna of Ounianga, only the endobenthic *M. tuberculata* is strongly influenced by substrate quality (Lévêque *et al.*, 1983). Substrate type may explain why it is currently found only in L. Boku, which has, for Ounianga, an atypical substrate of sand rather than calcareous organic muds (coarse sand >150 μm represents 49% of total dry weight, vs. 0–5% in other lakes). The flocculent fine-grained mud characterising the other lakes' bottom substrate is probably hypoxic or anoxic, and hence unfavourable for endobenthic snails. The other species live mostly on vegetation and hence are less affected by the type of substrate. The most species-rich freshwater gastropod communities typically occur in association with submerged and emergent macrophytes, because then both large epibenthic as well as small epiphytic species are represented (Brown, 1994). The early Holocene mollusc fauna at Ounianga consisted mainly of species indicative for diverse submerged aquatic vegetation. Species such as *A. coretus* and *G. costulatus* depend on aquatic plants and hence their presence during the early Holocene indicates calm (i.e. not turbulent or wind-swept) nearshore waters with abundant aquatic plants. Modern conditions in the Ounianga lakes meet these requirements only in Boku and Girki, where rooted *Phragmites* and *Potamogeton* beds occur on a stable bottom with low detritus/organic matter content and good light penetration. Light and oxygen availability are evidently less favourable beneath and between the floating *Phragmites* mats covering much of the current lakes at Ounianga Serir. Elsewhere in (sub)tropical Africa, standing waters covered for a large part by floating vegetation such as *Phragmites* or *Papyrus* are typically poor in molluscs (often only *Pila* and *Biomphalaria*), owing to the unfavourable combination of flocculent mud/detritus bottoms, the lack of light and periodic water column anoxia due to the immobilisation of water among and below swampy vegetation (Beadle, 1981; Van Damme and Van Bocxlaer, 2009). However, also the Ounianga lakes which are only partly reed-covered have open surfaces of clear and oxygenated water (Fig. 1c), where macrophyte beds should be able to develop. The apparent absence of *Biomphalaria* from all lakes except Boku, despite its tolerance to the environmental stresses presented by floating reed mats, refutes a primary role of these mats in shaping the modern aquatic mollusc community at Ounianga.

The early Holocene mollusc fauna at Ounianga and other Saharan localities

Table 7 lists the early Holocene fauna of the Ounianga lakes and other Late Pleistocene–early Holocene sites across the present-day Sahara. In contrast to hydrologically well-connected waters (Chad Basin, Wadi Howar, Basin de Taoudenni), the early Holocene fauna of Ounianga strongly resembles that of perennial but isolated Saharan waters such as the oases of Bir Sahara and Bir Tarfawi, crater lakes in the Tibesti (e.g. Trou au

Table 7. Comparison of the Late Pleistocene–early Holocene malacofauna of the Chad Basin when occupied by Lake Mega-Chad (Germain, 1935; Llabador, 1962, unpublished 1968; Lévêque, 1967; Böttcher *et al.*, 1972; Van Damme, 1984; Van Damme and Van Bocxlaer, 2009), the Wadi Howar in Sudan (Kröpelin, 1993), the Basin de Taoudenni in Mali (Rosso, 1983), isolated ponds and piedmont lakes in the Hoggar, Algeria (Sparks and Grove, 1961; Van Damme, 1984) and in the Tibesti Mountains (Germain, 1936; Sparks and Grove, 1961; Jaeckel, 1972; Van Damme, 1984), the Ounianga lakes (this study), isolated oases in the Libyan Desert (Gabriel, 1986; Girod, 1998) and Bir Sahara and Bir Tarfawi in the Western Desert of Egypt (Gautier, 1980, 1993).

	Aff.	Chad Basin	Wadi Howar	Basin de Taoudenni	Hoggar	Tibesti	Ounianga	Libyan Desert	Bir Sahara/ Bir Tarfawi
Gastropoda Caenogastropoda									
Viviparidae									
<i>Bellamyia unicolor</i>	A	x/m	–	x	–	–	–	–	–
Ampullariidae									
<i>Pila ovata</i>	A	x	x	–	–	–	–	–	–
<i>Pila wernei</i>	A	x/m	–	–	–	–	–	–	–
<i>Lanistes carinatus</i>	A	–/m	x	–	–	–	–	–	–
<i>Lanistes ovum</i>	A	x/m	–	–	–	–	–	–	–
Hydrobiidae									
<i>Hydrobia ventrosa</i>	P	–	–	–	x	x	–	x	(?)
Bithyniidae									
<i>Gabbiella senaariensis</i>	A	x/m	x	–	–	–	–	–	–
<i>Gabbiella tchadiensis</i>	A/E	x/m	–	–	–	–	–	–	–
<i>Gabbiella ouniangaensis</i>	A/E	–	–	–	–	–	x	–	–
Thiaridae									
<i>Melanoides tuberculata</i>	A	x/m	x	x	x	x/m	x/m	x	x
Paludomidae									
<i>Cleopatra bulimoides</i>	A	x/m	x	x	–	–	x*	–	x*
Gastropoda Heterobranchia									
Valvatidae									
<i>Valvata nilotica</i>	P	x	x	–	–	x	x	x	–
Lymnaeidae									
<i>Lymnaea natalensis</i>	A	x/m	x	x	x	x	x/m	x	x
<i>Lymnaea truncatula</i>	P	–	–	–	x	x	–	–	–
Ancylidae									
<i>Ancylus fluviatilis</i>	P	–	–	–	–/m	–	–	–	–
<i>Ferrissia eburnensis</i>	A	–/m	–	–	–	–	–	–	–
Planorbidae									
<i>Africanogyrus coretus</i>	A	x/m	x	–	x	x	x	x	–
<i>Armiger crista</i>	P/Mt	–	–	–	x	x	–	–	–
<i>Ceratophallus natalensis</i>	A	–/m	–	x	–	–	–	–	–
<i>Ceratophallus bicarinatus</i>	A	–/m	–	–	–	–	–	–	–
<i>Gyraulus costulatus</i>	A	x/m	x	x	x	x	x	–	x
<i>Lentorbis benguelensis</i>	A	–/m	–	–	–	–	–	–	–
<i>Lentorbis junodi</i>	A	–/m	–	–	–	–	x	–	–
<i>Segmentorbis angustus</i>	A	x/m	x	x	x	x	–	x	–
<i>Segmentorbis kanisaensis</i>	A	x/m	–	–	–	–	–	–	–
<i>Biomphalaria alexandrina</i>	A	–	–	–	–	–	–	–	x
<i>Biomphalaria pfeifferi</i>	A	x/m	x	x	x/m	x/m	x/m	x	–
<i>Biomphalaria stanleyi</i>	A	–/m	–	–	–	–	–	–	–
<i>Biomphalaria sudanica</i>	A	x/m	–	–	–	–	–	–	–
<i>Biomphalaria tchadiensis</i>	A/E	x/m	–	–	–	–	–	–	–
<i>Bulinus jousseaumei</i>	A	–/m	–	–	–	–	–	–	–
<i>Bulinus umbilicatus</i>	A	–/m	–	–	–	–	–	–	–
<i>Bulinus obtusus</i>	A	–/m	–	–	–	–	–	–	–
<i>Bulinus truncatus</i>	A	x/m	x	x	x/m	x/m	x	x	x
<i>Bulinus forskali</i>	A	x/m	x	x	–	–	–	–	x
Bivalvia Heterodonta (Unionoida)									
Unionidae									
<i>Coelatura aegyptica</i>	A	x/m	x	x	–	–	–	–	–
<i>Coelatura gabonensis</i>	A	x/m	–	–	–	–	–	–	–
<i>Coelatura bangoranensis</i>	A/E	x/m	–	–	–	–	–	–	–
<i>Nitia teretiuscula</i>	A/E	–/m	–	x	–	–	–	–	–
<i>Nitia mutelaeformis</i>	A/E	–/m	–	–	–	–	–	–	–
Iridinidae									
<i>Aspatharia chaiziana</i>	A	x/m	–	–	–	–	–	–	–
<i>Aspatharia pfeifferiana</i>	A	–/m	–	–	–	–	–	–	–
<i>Chambardia rubens</i>	A	x/m	x	(?)	–	–	–	–	–
<i>Chambardia wismanni</i>	A	x/m	–	–	–	–	–	–	–
<i>Chambardia wahlbergi</i>	A	x/m	–	–	–	–	–	–	–

(Continues)

Table 7 (Continued)

	Aff.	Chad Basin	Wadi Howar	Basin de Taoudenni	Hoggar	Tibesti	Ounianga	Libyan Desert	Bir Sahara/Bir Tarfawi
<i>Chambardia tabula</i>	A	x/m	–	–	–	–	–	–	–
<i>Mutela dubia</i>	A	x/m	x	(?)	–	–	–	–	–
<i>Mutela joubini</i>	A	x/m	–	–	–	–	–	–	–
<i>Mutela rostrata</i>	A	–/m	–	–	–	–	–	–	–
Etheriidae									
<i>Etheria elliptica</i>	A	x/m	x	–	–	–	–	–	–
Bivalvia Heterodonta (Veneroidea)									
Corbiculidae									
<i>Corbicula fluminalis</i>	A	x/m	x	x	x	–	–	–	x
Pisidiidae									
<i>Sphaerium hartmanni</i>	A	x/m	–	–	–	–	–	–	–
<i>Pisidium pirothi</i>	A	x/m	–	–	–	–	–	–	–
<i>Pisidium subtruncatum</i>	P	x	–	–	–	–	–	–	–
<i>Pisidium ovampicum</i>	A	x	–	–	–	x	x	–	–
<i>Pisidium milium</i>	A	–	–	–	–	x	–	–	–
<i>Eupera ferruginea</i>	A	x/m	–	–	–	–	–	–	–
Caenogastropoda		8	5	3	2	2	3	2	3
Heterobranchia		11	8	7	8	9	7	6	5
Unionoidea		11	4	4	0	0	0	0	0
Veneroidea		6	1	2	1	2	1	0	1
Totals		36	18	16	11	13	11	8	9

Biogeographic affinities (Aff.) classified as Afrotropical (A), Palaearctic (P), Montane (Mt), currently endemic to the Chad Basin (E); presence in the fossil and modern fauna are indicated by x and m; question marks (?) indicate records identified to genus level only.

Natron), the Wadi Teshuinat in the Libyan desert and piedmont lakes in the Hoggar. Even during the early Holocene humid period, these waters lacked gastropods belonging to the Ampullariidae and Viviparidae families as well as bivalves of the Unionidae and Iridinidae, which all require good hydrological connectivity of surface waters for their dispersal (Gautier, 1980; Van Damme, 1984; Girod, 1998; Van Damme and Van Bocxlaer, 2009). Given that favourable mollusc habitat prevailed at Ounianga Serir in the early Holocene (see above), the absence of such molluscs at Ounianga Serir, while present in Lake Mega-Chad (Table 7), likely indicates the lack of a surface water connection allowing upstream colonisation from Lake Mega-Chad. Grenier *et al.* (2009) suggested that the early Holocene Lake Yoa at Ounianga Kebir probably was hydrologically open, with an outflow towards Lake Mega-Chad across a sill at 419 m above sea level (a.s.l.). However this open-basin scenario still requires examination through ground-truthing topographical and geomorphological survey. Likewise, such surveys have not been made for Ounianga Serir, but a comparable early Holocene hydrological connection to Lake Mega-Chad would have involved a putative river channel from Serir to Kebir across the 431 m a.s.l. outflow sill of Ounianga Serir, two additional thresholds at 425 and 428 m a.s.l. and two spillover basins (Fig. 4). This putative outflow channel was certainly less permanent than the outflow from Lake Yoa, since Ounianga Serir lacked the river inflow from the Tibesti Mountains which, according to Grenier *et al.* (2009), helped sustain the early Holocene open hydrology of Ounianga Kebir. Moreover, even if it did exist, the multiple upstream barriers and/or steep gradients appear to have been insurmountable for those species of freshwater molluscs (or their parasitised fish hosts) which depend on aquatic dispersal. Also, the effectiveness of the two spillover basins as stepping stones in the dispersal of aquatic organisms is questionable: their own catchment is relatively small (Fig. 4) and they do not benefit from direct contact with a large fossil groundwater aquifer. Given that the climatic moisture balance in the early and mid Holocene Sahara overall was still negative (Kröpelin *et al.*, 2008), a significant outflow from Ounianga Serir would have

been required to prevent their desiccation. Because mollusc-bearing early Holocene outcrops have thus far not been found at Ounianga Kebir, we cannot judge whether its freshwater mollusc fauna included species depending on aquatic dispersal. Aquatic systems with early Holocene habitat conditions similar to Ounianga Serir but better hydrographic connectivity existed in the Taoudenni Basin in Mali (Rosso, 1983) and the Wadi Howar in Sudan (Kröpelin, 1993). Besides a characteristically different mollusc assemblage (Table 7) these systems were also inhabited by other taxa requiring surface water connections for dispersal: various fish, turtles and, less conclusively, hippopotamus and crocodiles (Gayet, 1983; de Broin, 1983; Kröpelin, 1993).

As far as the aquatic molluscs are concerned (Table 7), the early Holocene Ounianga Serir was among the most diverse isolated aquatic ecosystems in the central Sahara. The mollusc fauna was composed of Afrotropical elements with modern-day distributions in sub-Saharan Africa, the Palaearctic element *Valvata nilotica* which at that time was widely distributed in the Tibesti, the Libyan Desert, the Wadi Howar and the Chad Basin (Van Damme, 1984), and one species, *Gabbiella ouniangaensis*, possibly endemic to Ounianga. The species composition of the early Holocene mollusc community of Ounianga Serir is most similar to that from early Holocene waters in the Tibesti, where all Ounianga species except *Gabbiella ouniangaensis* and *Lentorbis junodi* have been reported (although the *Segmentorbis* reported from the Tibesti may belong to *Lentorbis*; see remark in the Taxonomy subsection, above). The main difference is that isolated early Holocene high-elevation sites in the Tibesti and also the Hoggar provided more favourable conditions for Palaearctic taxa (four in Tibesti, three in Hoggar; Table 7), so that their overall species richness is nevertheless comparable to or slightly greater than that of Ounianga. Our discovery of a *Gabbiella* species new to science is surprising; however, the reason that it has not been reported from other Saharan localities may well be the limited attention paid to the diagnostic morphology of opercula in earlier studies. A comprehensive analysis of fossil *Gabbiella* opercula

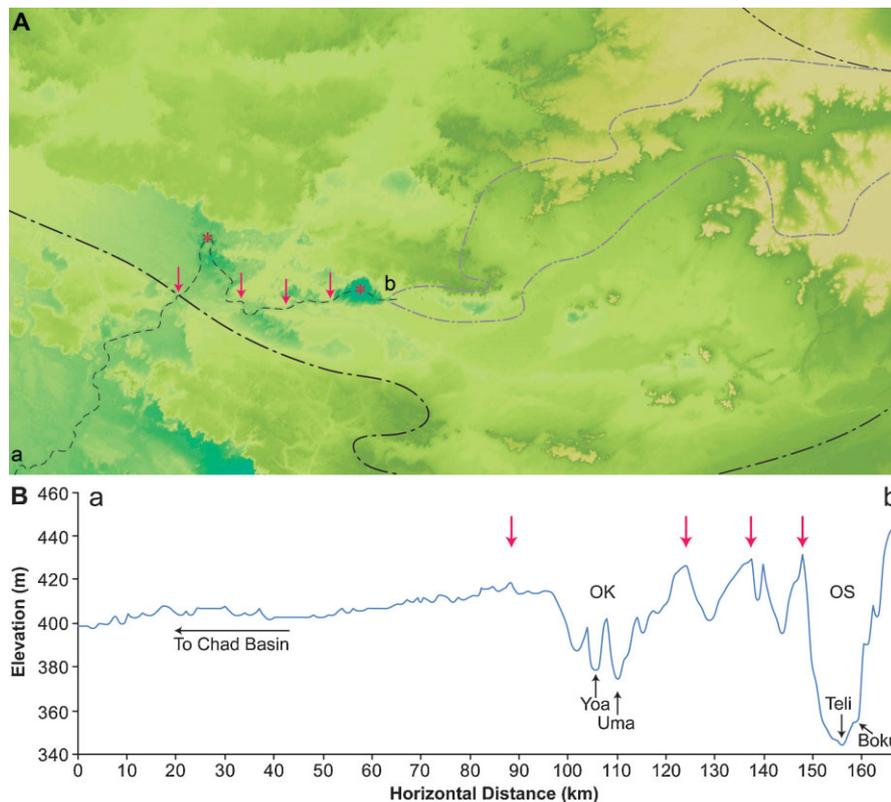


Figure 4. SRTM digital elevation model of the larger Ounianga region (A) with asterisks representing Lake Teli at Ounianga Serir (right) and Lake Yoa at Ounianga Kebir (left); compare with Fig. 1(B and C). The catchment of Ounianga Kebir (black dash-dotted line) is much larger (>20-fold) than that of Ounianga Serir (grey dash-dotted line) and includes regions in the Tibesti. Elevation data for the fine dotted line transect between a and b are represented in B. Arrows in A and B indicate threshold sills and their elevations (from left to right: 419, 425, 428 and 431 m a.s.l.). SRTM V4 DEM from Jarvis *et al.* (2008); catchments after Grenier *et al.* (2009). This figure is available in colour online at wileyonlinelibrary.com.

from the Sahara may reveal it to be a probably extinct species with widespread Late Pleistocene–early Holocene distribution.

Origin of the current mollusc fauna at Ounianga

The current freshwater mollusc fauna of Ounianga consists of small populations of only three species: *Melanoides tuberculata* and *Biomphalaria pfeifferi* in L. Boku and *Lymnaea natalensis* in the Girki creek and in L. Djara, with dwarfism at least in *L. natalensis*. Moreover, both *B. pfeifferi* and *L. natalensis* occur in very small populations, unlike the high abundances they regularly achieve elsewhere (Brown, 1994). The restricted occurrence of a coarse-sand substrate may explain the limitation of *M. tuberculata* to Lake Boku but, as explained above, habitat limitations do not seem to explain the rarity and scattered distribution of the other two species. One aspect of the modern fauna is peculiar: *Bulinus truncatus* currently occurs both in the Tibesti and Hoggar, but is absent from the Ounianga lakes, and vice versa for *L. natalensis*. The absence of *B. truncatus* from Ounianga today is striking because of its general eurytopic nature and because, like *B. pfeifferi*, it can withstand long periods of seasonal desiccation, whereas *L. natalensis* and *M. tuberculata* cannot (Girod, 1998). *B. truncatus* and *B. pfeifferi* are also more tolerant to fluctuating temperature and chemical conditions than *L. natalensis*. The opportunistic species *B. truncatus*, *B. pfeifferi* and *M. tuberculata* are the most common and widespread aquatic molluscs in the central Sahara (Van Damme, 1984). In contrast, *L. natalensis* presently occurs only in sub-Saharan regions (Van Damme, 1984; Brown, 1994), and our finds at Ounianga represent the first record of modern

L. natalensis in the central Sahara. The current composition of the mollusc fauna at Ounianga is thus difficult to relate to that of the early Holocene Ounianga lakes based on differential survival resulting from ecological selection.

Therefore, the possibility that the modern-day aquatic mollusc fauna at Ounianga represents an impoverished surviving contingent of the local early Holocene fauna appears unlikely. This is all the more so since the persistence of freshwater habitat in the complex basin of Ounianga Serir depends on a fragile balance of effective isolation from saline waters without desiccation. More likely, the modern fauna represents a series of relatively recent colonisation events (natural and/or anthropogenic) in which species occurrences result mainly from stochasticity in long-distance dispersal and in the establishment of incipient populations in a geographically isolated habitat.

The actual dynamics of long-distance dispersal in natural communities remain poorly understood, despite the impact of dispersal on ecological and evolutionary processes (Vanschoenwinkel *et al.*, 2008). Surface water connections, animals and wind are the three principal vectors for dispersal of freshwater invertebrates (Bilton *et al.*, 2001). The relative dispersal capacity of individual taxa can be observed directly by their sequence of arrival in newly created isolated waters or by capturing organisms and their vectors during transport (Maguire, 1963), or it can be inferred from patterns of genetic differentiation between geographically isolated populations (Bossart and Prowell, 1998; DeJong *et al.*, 2001). However, expanding the results of such studies to geological timescales remains a major challenge in palaeoecology and the historical biogeography of aquatic biota. So far, evidence for dispersal

over long distances by animal vectors other than humans remains largely circumstantial. Some aquatic organisms possess clear mechanisms for dispersal in the absence of hydrographic connections, while for others such mechanisms must be inferred to explain their modern-day biogeographical distribution (Figueroa and Green, 2002; Frisch *et al.*, 2007), or the peculiar species composition of isolated faunas (Vagvolgyi, 1975). Among non-marine aquatic molluscs, living populations of Hydrobiidae, Bithyniidae, Valvatidae, some Melanopsidae and Thiaridae (such as *Melanoides tuberculata*), many pulmonate snails and clams of the superfamily Corbiculoidea have been recorded from isolated localities such as crater lakes, desert oases and rockpools (Pilsbry and Bequaert, 1927; Mandahl-Barth, 1954; Van Damme, 1984; Brown, 1994). Some molluscs are specifically adapted for passive dispersal by wind or animals such as waterfowl, aquatic insects and humans by a particular reproductive strategy or by the production of drought-resistant eggs or resting stages (Van Damme and Van Bocxlaer, 2009). A famous example in gastropods is the ancient transatlantic colonisation of Africa by South American *Biomphalaria* species (e.g. Bandoni *et al.*, 1995; DeJong *et al.*, 2001). Migrating birds in particular can play a prominent role in long-distance dispersal in the Sahara, where a precious few favourable stop-over sites are separated by a vast uninhabitable landscape. Some migratory bird species like sandgrouse (*Pterocles* sp.) have abdominal feathers anatomically adapted to absorb, retain and transport water (e.g. Maclean, 1983); such birds appear ideal carriers of propagules of freshwater organisms.

All mollusc species in both the early Holocene and present-day mollusc fauna at Ounianga, except perhaps *C. bulimoides* (no data available), have a documented capacity of long-distance dispersal in the absence of direct hydrographic connections (Van Damme, 1984; Wesselingh *et al.*, 1999; Facon *et al.*, 2003; Green and Figueroa, 2005; Ben-Ami and Heller, 2007; Van Damme and Van Bocxlaer, 2009). Consequently, Ounianga Serir required no passable surface connection to Lake Mega-Chad to develop its species-rich early Holocene mollusc fauna, and no continuity through time of the freshwater ecosystems at Ounianga is required to explain the presence of freshwater molluscs there today. The latter conclusion may even hold for its resident fish fauna: the two small cichlid fishes *Hemichromis letourneuxi* and *Sarotherodon galilaeus borkuanus* are both widely distributed across the Sahara, and their occurrence in isolated crater and oasis lakes (Loiselle, 1992; Schliewen, 2005) suggests a capacity for passive dispersal (J. Snoeks, Royal Museum of Central Africa, Tervuren, pers. comm. 2009). In Ounianga Kebir, Lake Yoa became hypersaline around 3800 cal. a BP (Kröpelin *et al.*, 2008) and subsequent freshwater habitats have almost certainly been restricted to small spring-fed creeks if these existed continuously. The demonstrated continuity of Lake Yoa throughout the arid late Holocene, moreover, has no bearing on the situation for the shallower lakes at Ounianga Serir, which appear to be subject to a different balance of groundwater inflow to lake surface evaporation.

In summary, complete absence in the early Holocene freshwater ecosystem at Ounianga Serir of mollusc species requiring hydrographic connections for their dispersal suggests that early Holocene surface connections between Ounianga and Lake Mega-Chad either did not allow upstream migration of molluscs and other taxa, e.g. due to steep flow gradients or an ephemeral nature of the connection, or that Ounianga Serir was not hydrologically connected. A conclusive statement about whether sizable freshwater environments at Ounianga Serir existed continuously throughout the dry late Holocene cannot be made at this point. However, the paucity of the current

mollusc fauna despite diverse and seemingly favourable habitat conditions, as well as its characteristic species composition and the fragile hydrological balance at Ounianga Serir, suggest that the fauna was established relatively recently through new colonisations following a complete eradication of the early Holocene fauna.

Acknowledgements. This research was supported by the Research Foundation of Flanders (FWO-Vlaanderen), the Ghent University research council (UGent-BOF) and the Deutsche Forschungsgemeinschaft (SFB 389 – ACACIA). We thank Baba Mallaye of the Centre National d'Appui à la Recherche of Chad for research permission, Jos Snoeks for identification of Ounianga fish, Eric Coppejans for access to optical instrumentation, and Dirk Van Damme, Hilde Eggermont, Ilse Bessems, Kay Van Damme and Achilles Gautier for discussions and advice. BVB is Aspirant of the FWO-Vlaanderen.

References

- Appleton CC. 1978. Review of literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. *Malacological Review* **11**: 1–25.
- Appleton CC, Eriksson IM. 1984. The influence of fluctuating above-optimal temperature regimes on the fecundity of *Biomphalaria pfeifferi*. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **78**: 49–54.
- Bandoni SM, Mulvey M, Loker ES. 1995. Phylogenetic analysis of eleven species of *Biomphalaria* Preston, 1910 (Gastropoda: Planorbidae) based on comparisons of allozymes. *Biological Journal of the Linnean Society* **54**: 1–27.
- Bayly IAE. 1972. Salinity tolerance and osmotic behavior of animals in athalassic saline and marine hypersaline waters. *Annual Review of Ecology and Systematics* **3**: 233–268.
- Beadle LC. 1981. *The Inland Waters of Tropical Africa: An Introduction to Tropical Limnology* (2nd edn). Longman: London.
- Ben-Ami F, Heller J. 2005. Spatial and temporal patterns of parthenogenesis and parasitism in the freshwater snail *Melanoides tuberculata*. *Journal of Evolutionary Biology* **18**: 138–146.
- Ben-Ami F, Heller J. 2007. Temporal patterns of geographic parthenogenesis in the freshwater snail. *Biological Journal of the Linnean Society* **91**: 711–718.
- Bilton DT, Freeland JR, Okamura B. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* **32**: 159–181.
- Bitakaramire PK. 1968. The survival of *Lymnaea natalensis* in drought conditions. *Bulletin of Epizootic Diseases of Africa* **16**: 473–475.
- Bossart JL, Powell DP. 1998. Genetic estimates of population structure and gene flow: limitations, lessons and new directions. *Trends in Ecology and Evolution* **13**: 202–206.
- Böttcher UP, Ergenzinger P, Jaeckel SH, *et al.* 1972. Quartäre Seebildungen und ihre Mollusken Inhalte im Tibesti-Gebirge und seinen Rahmenbereichen der Zentralen Ost-Sahara. *Zeitschrift für Geomorphologie NF* **16**: 182–234.
- Bouchet P, Rocroi J-P, Frýda J, *et al.* 2005. Classification and nomenclator of gastropod families. *Malacologia* **47**: 1–397.
- Brinkmann PJ, Heintz M, Holländer R, Reich G. 1987. Retrospective simulation of groundwater flow and transport in the Nubian Aquifer System. *Berliner geowissenschaftliche Abhandlungen (A)* **75**: 465–516.
- Brown DS. 1994. *Freshwater Snails of Africa and their Medical Importance* (rev. 2nd edn). Taylor & Francis: London.
- Brown DS, Mandahl-Barth G. 1973. Two new genera of Planorbidae from Africa and Madagascar. *Proceedings of the Malacological Society of London* **40**: 287–302.
- Brown DS, Fison T, Southgate VR, *et al.* 1984. Aquatic snails of the Jonglei region, southern Sudan, and transmission of trematode parasites. *Hydrobiologia* **110**: 247–271.
- Castañeda IS, Mulitza S, Schefuß E, *et al.* 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proceedings of the National Academy of Sciences of the USA* **106**: 20159–20163.

- Claussen M, Gayler V. 1997. The greening of the Sahara during the Mid-Holocene: results of an interactive atmosphere–biome model. *Global Ecology and Biogeography Letters* **6**: 369–377.
- Cridland CC. 1967. Resistance of *Bulinus globosus*, *B. africanus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* to experimental desiccation. *Bulletin of the World Health Organization* **36**: 507–513.
- de Broin F. 1983. Chéloniens. In *Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali)*, Petit-Maire N, Riser J (eds). Centre National de la Recherche Scientifique: Marseille; 211–234.
- DeJong RJ, Morgan JAT, Paraense L, et al. 2001. Evolutionary relationships and biogeography of *Biomphalaria* (Gastropoda: Planorbidae) with implications regarding its role as host of the human bloodfluke *Schistosoma mansoni*. *Molecular Biology and Evolution* **18**: 2225–2239.
- De Kock KN, Van Eeden JA. 1981. Life table studies on freshwater snails: the effect of constant temperature on the population dynamics of *Biomphalaria pfeifferi* (Krauss). *Wetenskaplike Bydraes van die Potchefstroomse Universiteit, B: Natuurwetenskappe* **107**: 1–17.
- deMenocal P, Ortiz J, Guilderson T, et al. 2000. Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. *Quaternary Science Reviews* **19**: 347–361.
- Donnelly FA, Appleton CC. 1985. Observations on the field transmission dynamics of *Schistosoma mansoni* and *S. mattheei* in southern Natal, South Africa. *Parasitology* **91**: 281–290.
- Edmunds WM, Dodo A, Djoret D, et al. 2004. Groundwater as an archive of climatic and environmental change: Europe to Africa. In *Past Climate Variability through Europe and Africa. Series: Developments in Paleoenvironmental Research*, Vol. 6, Battarbee RW, Gasse F, Stickley CE (eds). Springer: Berlin; 279–306.
- Eggermont H, Russell JM, Schettler G, et al. 2007. Physical and chemical limnology of alpine lakes and pools in the Rwenzori Mountains (Uganda–DR Congo). *Hydrobiologia* **592**: 151–173.
- Eggermont H, Verschuren D, Fagot M, et al. 2008. Aquatic community response in a groundwater-fed desert oasis to Holocene desiccation of the Sahara. *Quaternary Science Reviews* **27**: 2411–2425.
- Facon B, Pointier JP, Glaubrecht M, et al. 2003. A worldwide molecular phylogeography approach to biological invasions in parthenogenetic thiarid snails. *Molecular Ecology* **12**: 3027–3041.
- Figuerola J, Green AJ. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology* **47**: 483–494.
- Frisch D, Green AJ, Figuerola J. 2007. High dispersal capacity of a broad spectrum of aquatic invertebrates via waterbirds. *Aquatic Sciences* **69**: 568–574.
- Gabriel B. 1986. Die östliche Libysche Wüste im Jungquartär. *Berliner Geographische Studien* **19**: 1–216.
- Gautier A. 1980. Contributions to the archaeozoology of Egypt. In *Prehistory of the Eastern Sahara*, Wendorf F, Schild R (eds). Academic Press: New York; 317–339.
- Gautier A. 1993. The Middle Paleolithic Archaeofaunas from Bir Tarfawi (Western Desert, Egypt). In *Egypt during the Last Interglacial: The Middle Paleolithic of Bir Tarfawi and Bir Sahara East*, Wendorf F, Schild R, Close AE, and associates (eds). Plenum Press: New York; 121–143.
- Gayet M. 1983. Poissons. In *Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali)*, Petit-Maire N, Riser J (eds). Centre National de la Recherche Scientifique: Marseille; 183–210.
- George U, Kröpelin S. 2000. Entdeckungen im Herzen der Leere: eine Expedition in den Nordost-Tschad. *Forschung in Köln* **1/2000**: 66–75.
- Genner MJ, Michel E, Todd JA. 2008. Resistance of an invasive gastropod to an indigenous trematode parasite in Lake Malawi. *Biological Invasions* **10**: 41–49.
- Germain L. 1935. La Faune malacologique du lac Tchad et des Pays Bas du Tchad. *Archives du Muséum national d'Histoire naturelle, Paris, 6e série, XII* **2**: 389–400.
- Germain L. 1936. Mollusques fluviatiles du Tibesti. *Mémoires de l'Académie des Sciences Paris* **62**: 53–63.
- Girod A. 1998. Molluscs and palaeoenvironment of Holocene lacustrine deposits in the erg Uan Kasa and in the Edeyen of Murzuq (Libyan Sahara). In *Wadi Teshuinat: Palaeoenvironment and Prehistory in South-western Fezzan (Libyan Sahara)*, Cremaschi M, Di Lernia S (eds). Firenze Stampa: Florence; 73–88.
- Gorham E, Dean WE, Sanger JE. 1983. The chemical composition of lakes in the north-central United States. *Limnology and Oceanography* **28**: 287–301.
- Green AJ, Figuerola J. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. *Diversity and Distributions* **11**: 149–156.
- Grenier C, Paillou P, Maugis P. 2009. Assessment of Holocene surface hydrological connections for the Ounianga lake catchment zone (Chad). *Comptes Rendus Geoscience* **8-9**: 770–782.
- Grétilat S, Gaston G. 1975. Sur quelques particularités écologiques de la faune malacologique vectrice de trématodes dans les Dallols nigériens. *Annales de Parasitologie, Paris* **50**: 595–601.
- Griffin DL. 2006. The late Neogene Sahabi Rivers of the Sahara and their climatic and environmental implications for the Chad Basin. *Journal of the Geological Society, London* **163**: 905–921.
- Hammer UT. 1986. *Saline Lake Ecosystems of the World*. W. Junk: Dordrecht.
- Hesse KH, Hissene A, Kheir O, et al. 1987. Hydrogeological investigations in the Nubian Aquifer System, Eastern Sahara. *Berliner geowissenschaftliche Abhandlungen (A)* **75**: 397–464.
- Hissene AM. 1986. Géologie und Hydrogéologie des Erdis-Beckens, NE-Tschad. *Berliner geowissenschaftliche Abhandlungen (A)* **76**: 1–67.
- Hoelzmann P, Gasse F, Dupont LM, et al. 2004. Palaeoenvironmental changes in the arid and sub arid belt (Sahara-Sahel-Arabian Peninsula) from 150 kyr to present. In *Past Climate Variability through Europe and Africa. Series: Developments in Paleoenvironmental Research*, Vol. 6, Battarbee RW, Gasse F, Stickley CE (eds). Springer: Dordrecht; 219–256.
- Jaekel SH. 1972. Quartäre Mollusken aus Seeabsätzen des Tibesti-Gebirges. *Zeitschrift für Geomorphologie NF* **16**: 211–220.
- Jarvis A, Reuter HI, Nelson A, et al. 2008. Hole-filled SRTM for the globe Version 4. CGIAR-CSI SRTM 90m database. Available: <http://srtm.csi.cgiar.org> [11 December 2010].
- Kröpelin S. 1993. Zur Rekonstruktion der spätquartären Umwelt am Unteren Wadi Howar (Südöstliche Sahara / NW-Sudan). *Berliner Geographische Abhandlungen* **54**: 1–293.
- Kröpelin S. 2007. The Saharan lakes of Ounianga Serir: a unique hydrological system. In *Atlas of Cultural and Environmental Change in Arid Africa*, Bubenzer O, Bolten A, Darius F (eds). Heinrich-Barth-Institut: Köln; 54–55.
- Kröpelin S, Verschuren D, Lézine AM, et al. 2008. Climate-driven ecosystem succession in the Sahara: the last 6000 years. *Science* **320**: 765–768.
- Lévêque C. 1967. Mollusques aquatiques de la zone du lac Tchad. *Bulletin de l'institut fondamental d'Afrique Noire* **29**: 1494–1533.
- Lévêque G, Dejoux C, Lauzanne L. 1983. The benthic fauna: ecology, biomass and communities. In *Lake Chad: Ecology and Productivity of a Shallow Tropical Ecosystem*, Carmouze JP, Durand JR (eds). W. Junk: The Hague; 233–272.
- Llabador F. 1962. *Résultats malacologiques de la mission scientifique du Ténére (Novembre 1959–Janvier 1960)*. Mission Berliet Ténére-Tchad. Documents scientifiques Paris, CNRS; 235–269.
- Loiselle PV. 1992. An annotated key to the genus *Hemichromis* Peters 1958. *Buntbarsche Bulletin* **148**: 2–19.
- Maclean GL. 1983. Water transport by sandgrouse. *Bioscience* **33**: 365–369.
- Madsen H. 1992. Food selection by freshwater snails in the Gezira irrigation canals, Sudan. *Hydrobiologia* **228**: 203–217.
- Maguire B. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecological Monographs* **33**: 161–185.
- Maley J. 2000. Last Glacial Maximum lacustrine and fluvial formations in the Tibesti and other Saharan mountains, and large-scale climatic teleconnections linked to the activity of the Subtropical Jet Stream. *Global and Planetary Change* **26**: 121–136.
- 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. 1968. Revision of the African Bithyniidae (Gastropoda Prosobranchia). *Extrait de la revue de zoologie et de botanique Africaines* **78**: 129–160.
- Mandahl-Barth G. 1988. *Studies on African freshwater bivalves*. Danish Bilharziasis Laboratory: Charlottenlund.
- McCullough FS. 1962. Further observations on *Bulinus* (*Bulinus*) *truncatus rohlfi* (Clessin) in Ghana: seasonal population fluctuation and Biology. *Bulletin of the World Health Organization* **27**: 161–170.
- Meier-Brook C, Haas D, Winter G, et al. 1987. Hydrochemical factors limiting the distribution of *Bulinus truncatus* (Pulmonata: Planorbidae). *American Malacological Bulletin* **5**: 85–90.
- Özdikmen H, Darilmaz MB. 2007. *Africanogyris* nom. n., a replacement name for the preoccupied snail genus *Afrogyris* Brown & Mandahl-Barth, 1973 (Gastropoda: Planorbidae). *African Invertebrates* **48**: 259–260.
- Pachur HJ, Altmann N. 2006. *Die Ostsahara im Spätquartär*. Springer: Berlin.
- Pesce A. 1968. *Gemini Space Photographs of Libya and Tibesti: A Geological and Geographical Analysis*. Petroleum Exploration Society of Libya: Tripoli.
- Pilsbry H, Bequaert J. 1927. The aquatic molluscs of the Belgian Congo. *Bulletin of the American Museum of Natural History* **53**: 69–602.
- Reimer PJ, Baillie MGL, Bard E, et al. 2004. IntCal04 Terrestrial radiocarbon age calibration, 26-0 ka BP. *Radiocarbon* **46**: 1029–1058.
- Rosso JC. 1983. Mollusques. In *Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali)*, Petit-Maire N, Riser J (eds). Centre National de la Recherche Scientifique: Marseille; 157–172.
- Samadi S, Mavarez J, Pointier JP, et al. 1999. Microsatellite and morphological analysis of population structure in the parthenogenetic freshwater snail *Melanooides tuberculata*: insights in the creation of clonal variability. *Molecular Ecology* **8**: 1141–1153.
- Schliewen UK. 2005. Cichlid species flocks in small Cameroonian lakes. In *Freshwater Ecoregions of Africa and Madagascar*, Thieme ML, Abell R, Stiassny MLJ, Skelton P, Lehner B et al. (eds). Island Press: London; 58–60.
- Schutte CHJ, Frank GH. 1964. Observations on the distribution of freshwater Mollusca and chemistry of the natural waters in the southeastern Transvaal and adjacent northern Swaziland. *Bulletin of the World Health Organization* **30**: 389–400.
- Shiff CJ. 1966. The influence of temperature on the vertical movement of *Bulinus* (*P.*) *globosus* in the laboratory and in the field. *South African Journal of Science* **62**: 210–214.
- Sparks BW, Grove AT. 1961. Some Quaternary fossil non-marine Mollusca from the central Sahara. *Journal of the Linnean Society, Zoology* **44**: 355–364.
- Stuiver M, Reimer PJ. 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. *Radiocarbon* **35**: 215–230.
- Thomson FG. 1984. *Freshwater Snails of Florida: A Manual for Identification*. University of Florida Press: Gainesville, FL.
- Trewavas E, Teugels GG. 1991. Sarotherodon. In *Check-List of the Freshwater Fishes of Africa (CLOFFA)*, Vol. 4, Daget J, Gosse JP, Teugels GG, Thys van den Audenaerde DFE (eds). MRAC: Tervuren/ORSTOM: Paris; 425–437.
- Utzinger J, Tanner M. 2000. Microhabitat preferences of *Biomphalaria pfeifferi* and *Lymnaea natalansis* in a natural and a man-made habitat in Southeastern Tanzania. *Memórias do Instituto Oswaldo Cruz* **95**: 287–294.
- Vagvolgyi J. 1975. Body size, aerial dispersal, and origin of the Pacific land snail fauna. *Systematic Zoology* **24**: 465–488.
- Van Damme D. 1984. *The Freshwater Mollusca of Northern Africa: Distribution, Biogeography and Palaeoecology*. W. Junk: Dordrecht.
- Van Damme D, Van Bocxlaer B. 2009. Freshwater molluscs of the Nile Basin, past and present. In *The Nile: Origin, Environments, Limnology and Human Use*, Dumont HJ (ed.). *Monographiae Biologicae* **89**: 585–629.
- Vanschoenwinkel B, Gielen S, Seaman M. et al. 2008. Any way the wind blows-frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* **117**: 125–134.
- Verschuren D, Tibby J, Sabbe K, et al. 2000. Effects of lake level, salinity and substrate on the invertebrate community of a fluctuating tropical lake. *Ecology* **81**: 164–182.
- Wesselingh FP, Cadée GC, Renema W. 1999. Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. *Geologie en Mijnbouw* **78**: 165–174.
- Wilcox CD, Dove SB, McDavid WD, et al. 2002. *ImageTool 3.00 for Windows*, written using Borland's C++ version 5.0.2; developed in the Department of Dental Diagnostic Science at University of Texas Health Science Center, San Antonio, TX.
- Williams NV. 1970. Studies on aquatic Pulmonate snails in Central Africa. 1. Field distribution in relation to water chemistry. *Malacologia* **10**: 153–164.
- Wolff JP. 1964. *Carte Géologique de la République de Tchad*. Bureau de Recherches Géologiques et Minières: Orléans.
- Wollheim WM, Lovvorn JR. 1995. Salinity effects on macroinvertebrate assemblages and waterbird food webs in shallow lakes of the Wyoming High Plains. *Hydrobiologia* **310**: 207–223.
- Zhadin VI. 1965. Mollusks of Fresh and Brackish Waters of the U.S.S.R. In *Keys to the Fauna of the USSR*, Finesilver R (ed.). Israel Program for Scientific Translations [English translation of: Zhadin (1952) by A Mecado]: Jerusalem; 1–368.