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Daphnia species diversity in Kenya, and a key to the identification of their ephippia

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Abstract

The distribution of *Daphnia* species in tropical Africa is poorly known and understood. *Daphnia* are assumed rare in tropical regions, but systematic studies covering large areas are sparse. We sampled the active community (live zooplankton) and/or the dormant community (diapausing egg banks in the sediment) of 41 standing water bodies in Kenya in search for *Daphnia*. Overall the dormant communities yielded 11 species of *Daphnia*, a species richness more than twice the species richness found in the active communities. Dormant community species diversity better reflects the spatial, and particularly the temporal (multi-annual) variation in environmental conditions available to *Daphnia* in these tropical standing waters. Hence, we suggest that the dormant community be taken into account when assessing local zooplankton diversity, especially in fluctuating tropical lake ecosystems, where the presence of each local *Daphnia* species in the active community may be strongly seasonal or erratic. Geographic distribution data from this study are supplemented with previous records of *Daphnia* in East Africa to provide an overview of the known distribution of *Daphnia* in Kenya and neighbouring countries. We also present a detailed key for morphological identification of the ephippia of the 11 *Daphnia* species encountered, complemented with photographs and drawings of diagnostic characters.

Introduction

In many aquatic ecosystems, temporal habitat instability is a major factor determining zooplankton community composition at any given time. Different zooplankton taxa often show strong changes in abundances with time and space, depending on the prevailing conditions. As a result, the total zooplankton diversity can not be assessed by sampling at a single point in time or space. Rather, multiple sampling throughout the year is needed during the course of a growing season and, preferrably, covering several years. In order to cope with this temporal habitat instability many cladocerans produce resistant dormant stages that can survive unfavourable conditions and that can stay viable for years, even decades and longer (Cáceres, 1998). Sampling the dormant community from the sediment may therefore allow an assessment of the total species diversity of the local cladoceran community from a single sampling event (May, 1986; Havel et al., 2000; Vandekerkhove et al., submitted), provided that these dormant stages can be identified to species. Remains of cladocerans recovered from subrecent and older sediments include the ephippia of these dormant eggs but also mandibles and post-abdominal claws, and all have long been used in paleolimnological studies (e.g., Kitchell & Kitchell, 1980; Leavitt et al., 1989; Hann et al., 1994; Kerfoot et al., 1999). Unfortunately, since most local studies deal with ephippia of only a few species, which are related directly to the species present in the local active population, specific information regarding species identification of ephippia is mostly lacking or incomplete.

Most *Daphnia* species reproduce by cyclic parthenogenesis. Sexual reproduction occurs when living conditions are unfavourable or deteriorate (Carvalho & Hughes, 1983). During sexual reproduction the female carapace produces an ephippium around the brood chamber (Zaffagnini, 1987). Inside the ephippium a new cuticula is formed which encloses two embryos in arrested development. On both sides of the ephippium two convex swellings provide the necessary space for the dormant embryos. These swellings (hereforth called egg chambers) are more melanised than other parts of the ephippium and are often more sclerotised, and hence more resistant to physical damage. The ephippium is eventually released during the following moult, together with the old carapace (Zaffagnini, 1987). Because of their good preservation in lake sediments, ephippia are ideally suited for ecological and paleoecological studies.

Daphnia are considered rare in tropical regions, especially in the warm lowland tropics (Fernando et al., 1987; Dumont, 1994). Yet in equatorial East Africa *Daphnia* have been reported from a fairly large number of permanent lakes and ponds, with at least nine species found so far (Green, 1995). Previous regional studies (Green, 1971; Lehman, 1996) focused mostly on zooplankton diversity in the large East African Rift lakes. Small waterbodies, often of a semi-permanent or temporary nature, were often overlooked. Yet these habitats are often fishless, which is considered a key factor permitting the presence of *Daphnia* in tropical regions (Hebert, 1978; Dumont, 1994). We studied the dormant *Daphnia* community of 41 water bodies in Kenya, and compared its species diversity with that in the active community by simultaneous sampling of the live zooplankton. We also present a key for the identification of *Daphnia* species of Kenya and neighbouring regions, based on the morphology of ephippia.

Methods

Study area

Field surveys in August 2001 and January 2003 yielded collections of live zooplankton and recently deposited surface sediments from 41 standing water bodies in southern and southwestern Kenya. The sampled waters vary from small semi-permanent ponds and watering holes to larger lakes and dams (Table 1 and Fig. 1). The area is dissected from North to South by the Eastern Rift Valley. The surface elevation of the sampled waters varies from 700 to 1200 m a.s.l. in the southeastern lowlands (12 sites) to between 900 and 2800 m in the Rift Valley and adjacent escarpments (29 sites). In addition, we analysed ephippia extracted from previously studied sediment cores from the Lake Naivasha basin (Mergeay et al., submitted), and surface sediments of four lakes (Bandasa, Ellis, Nkunga, Simba) on Mt. Kenya (courtesy of Dr Philip Barker, Lancaster University, UK). This Mt. Kenya collection includes both high-elevation alpine lakes and lakes on the lower slopes of the mountain, with elevations ranging between 1800 and 4600 m. Overall, vegetation near the sampled waters ranges from dry *Acacia* bush land, grassland with scattered trees, highland forests and tropical rainforests to afromontane and alpine vegetation. Rainfall is strongly seasonal throughout the study region, predominantly bimodal to the East of the Kenyan Rift Valley and with a trimodal pattern in the West. Rainfall ranges from 350 mm in the arid southern savannah to 1100–1500 mm in the highlands (>1500 m). Mean temperature patterns are closely linked to altitude, and seasonal variation is very limited (Kiai et al., 2002).

Sampling

Water transparency was determined with a Secchi disc (20 cm diameter). Temperature and conductivity were determined in the middle of the water body using a Hydrolab multiprobe (Hydrolab Inc., USA). Geographical positioning and altitude measurement was done using a Garmin Global Positioning System (Garmin International Inc.).

Table 1. Sampling locations and presence of *Daphnia* species

Number	Name	Geographical coordinates	Alt (masl)	Secchi depth (m)	Temperature (°C)	Conductivity ($\mu S/cm^{-1}$)	Active community									Dormant community								
							barbata	laevis	curvirostris	pulex	sp. nov. type Limuru	magna	longispina s.l.	lumholtzi	dolichocephala	barbata	laevis	curvirostris	pulex	sp. nov. type Limuru	magna	longispina s.l.	lumholtzi	dolichocephala
1	Lake Challa	S 03° 19,0′ E37° 42,0′	842	13.00	27	324																		
2	Lake Jipe	S 03° 34.6′ E 37° 46,0′	735	0.30	28.5	1140																		
3	Temporary pond Taveta-Taita 1	S 03° 24,5′ E 38° 03,5′	1115	0.10	32.3	00										1								
4	Temporary pond Taveta-Taita 2	S 03° 24,6′ E 38° 002,2′	1103	0.10	28	150											1							
5	Temporary pond Taveta-Taita 3	S 03° 24,7′ E 37° 49,7′	1102	0.10	28.2	235																		
6	Permanent pond Voi-Nairobi 1	S 02° 45,4′ E 38° 15,3′	695	0.10	32.6	53																		
7	Permanent pond Voi-Nairobi 2	S 02° 21,0′ E 37° 53,3′	1031	0.10	31.5	236																		
8	Amboseli Olokenya swamp	S 02° 42,1′ E 37° 18,7′	1155	0.80	19.8	179																		
9	Amboseli Serena Lodge	S 02° 42,0′ E 37° 15,4′	1159	0.80	21.4	172																1		
10	Amboseli Enamishera	S 02° 40,2′ E 37° 14,6′	1150	0.80	24.7	255																		
11	Amboseli Lake Kioko	S 02° 38,5′ E 37° 13,5′	1153	0.50	25	539																		
12	Amboseli Lake Amboseli	S 02° 36,1′ E 37° 12,5′	1150	0.01	29.1	4690	1									1								
13	Temporary pond Kajiado	S 01° 50,2′ E 36° 47,9′	1757	0.25	24	150	1																	
14	Nairobi Nat. Park Narogomon dam	S 01° 21,0′ E 36°47,9′	1707	0.40	21.3	188		1									1							
15	Nairobi Nat. Park Hyena Dam	S 01° 20,3′ E 36° 48,6′	1709	0.30	21.7	260										1								
16	Nairobi Nat. Park 3	S 01° 21,9′ 36° 50,6′	1709	0.60	23	141										1								
17	Nairobi Nat. Park 4 (river)	S 01° 21,6′ E 36° 51,2′	1664	0.40	21	150																		
18	Nairobi Nat. Park Hyrax valley	S 01° 22.9′ E 36° 47,0′	1716	0.40	23.5	250																		
19	Temporary pond Limuru 1a	S 01° 7.0′ E 36° 37.9′	2306	0.15	21.5	201					1									1				
20	Temporary pond Limuru 1b	S 01° 7.0′ E 36° 37.9′	2306	0.15	21.5	201					1									1				
21	Permanent lake Limuru 2	S 01° 6,3′ E 36° 37,8′	2294	0.70	23.1	155		1			1						1		1	1				
22	Permanent Lake Limuru 3	S 01° 8,3′ E 36° 40.7′	2135	0.50	24.6	414																		
23	Lake Naivasha main	S 00° 46,3′ E 36° 21,7′	1897	0.20	22.9	292	1			1						1			1		1		1	
24	Lake Naivasha Crater	S 00° 45,8′ E 36° 24,6′	1897	1.20	22.5	375	1			1						1			1					

Table 1. (Continued)

Number	Name	Geographical coordinates	Alt (masl)	Secchi depth (m)	Temperature (°C)	Conductivity ($\mu S/cm^{-1}$)	Active community									Dormant community								
							barbata	laevis	curvirostris	pulex	sp. nov. type Limuru	magna	longispina s.l.	lumholtzi	dolichocephala	barbata	laevis	curvirostris	pulex	sp. nov. type Limuru	magna	longispina s.l.	lumholtzi	dolichocephala
25	Lake Oloidien	S 00° 48.9′ E 36° 15,9′	1897	0.30	23.3	2590															1			
26	Eldoret Sigawet Dam	N 00° 35,1′ E 35° 13,1′	2014	0.20	22.5	214										1	1		1					
27	Lake Katalin	N 00° 38,4′ E 35° 28,9′	2337	0.37	19.5	78																		
28	Permanent pond Eldoret Nakuru 1a	N 00° 26,4′ E 35° 18,3′	2185	0.50	14.1	196											1							
29	Permanent pond Eldoret Nakuru 1b	N 00° 26,4′ E 35° 18,3′	2185	0.30	16.2	381											1							
30	Permanent pond Eldoret Nakuru 2	N 00° 21,7′ E 35° 21,1′	2217	0.50	14.5	171											1							
31	Permanent pond Eldoret Nakuru 3	N 00°20,0′E 35° 21,9′	2214	0.40	16.2	221											1							
32	Lake Narasha	N 00° 2,6′ E 35° 32,4′	2764	2.20	16	34		1									1							
33	Permanent pond Eldoret Nakuru 5	S 00° 3.6′ E 35° 38,4′	2471	0.25	20.8	204											1							
34	Permanent pond Eldoret Nakuru 6	S 00° 4.9′ E 35° 39,5′	2536	0.10	24.5	117		1									1							
35	Permanent pond Nakuru Naivasha 1	S 00° 19,4′ E 36° 9.1′	1917	0.10	24	201																		
36	Permanent pond Nakuru Naivasha 2	S 00° 20,5′ E 36° 10,1′	1920	0.20	20.4	178																		
37	Lake Ol Bolossat	S 00° 9.9′ E 36° 25.9′	2358	0.20	20.6	1960	1				1					1	1		1	1	1			
38	Ol Bolossat pond 1	S 00° 10,1′ E 36° 26,0′	2350	0.20	19.5	250	1									1	1							
39	Ol Bolossat pond 2	S 00° 10,1′ E 36° 26,0′	2350	0.20	19.4	250	1									1	1							
40	Lake Banngo	N 00° 39,1′ E 36° 3,6′	967	0.05	26	1600	1									1	1		1					
41	Mogotio Kapchelukung Dam	N 00° 05′ E 36° 05′	1200	0.20	22.2	90	1									1	1							
42	Bandasa Mt Kenya	S 00° 09′ E 37° 28′	2900	> 1	18	20												1						1
43	Ellis Mt Kenya	?	3500	> 3	12.3	33																		1
44	Nkunga Mt Kenya	?	1840	> 1	16.2	316												1						
45	Simba Mt Kenya	?	4575	> 5	8.1	19																		

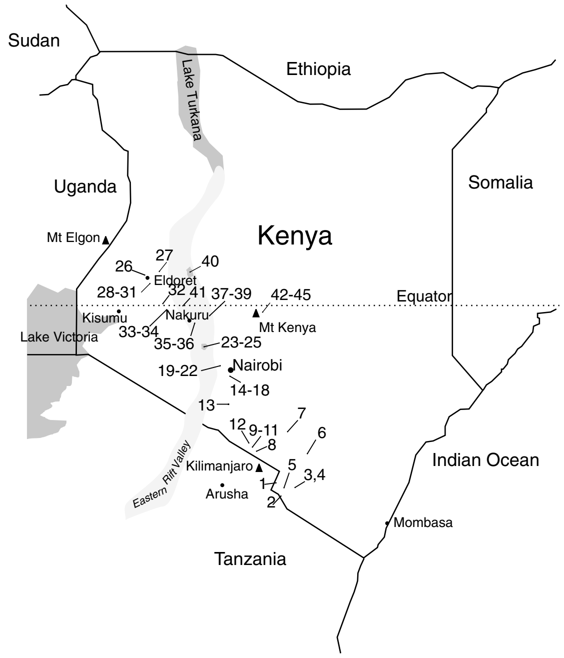

Figure 1. Map of Kenya with indication of sampling sites. Numbers refer to sample sites in Table 1.

Qualitative zooplankton samples were collected using a conical tow-net (25 cm diameter, 150 μm mesh), combining vertical hauls with horizontal hauls, and taking care to include zones with macrophytes and littoral vegetation. Samples were washed in the net and fixed in 100% ethanol. Offshore surface sediments were sampled from a boat using a weighted Wildco Fieldmaster® horizontal water sampler to ensure that only the topmost layer of flocculent mud was taken. In small ponds or very shallow water bodies, sediment was collected manually (~500 ml). These samples were stored without fixation.

In the laboratory, *Daphnia* in the zooplankton samples were identified using a compound microscope with reference to Kofinek (1999), and counted until 300 *Daphnia* had been processed; otherwise the whole sample was analysed. Subsamples of surface sediment were washed through a 250 μm mesh metal sieve, and the retained residue was scanned for *Daphnia* ephippia in a counting tray at 20–50 magnification. Ephippia were mainly identified using ephippial females in zooplankton reference collections.

Results

Of the 41 water bodies sampled, 27 contained *Daphnia*. Of these, 16 contained *Daphnia* in the live zooplankton, while in 25 of them *Daphnia* was found in the dormant egg bank (Table 1). In the active community only four species were found (*Daphnia barbata* Weltner, *Daphnia laevis* Birge, *Daphnia pulex* Leydig and a new undescribed species of the subgenus *Ctenodaphnia*, *Daphnia* sp. nov. type Limuru) while nine species were found in the sediment samples (*Daphnia barbata*, *Daphnia curvirostris* Eylman, *Daphnia longispina s.l.* O.F. Muller, *Daphnia laevis*, *Daphnia lumholtzi* Sars, *Daphnia magna* Straus, *Daphnia pulex*, *Daphnia cf. similis* Claus and *Daphnia* sp. nov. type Limuru). In addition *Daphnia dolichocephala* Sars was found in sediment samples from Mt Kenya. The average species richness was 1.6 species per lake that contained *Daphnia*. Four or more species were found in the recent sediment of three lakes (five in Lake Ol Bolossat and four in Lake Naivasha and Lake Limuru2) (Table 1). In many water bodies very few individuals were found however, in the active as well as in the dormant community. Those water bodies were mostly dominated by small cladocerans (*Moina*, *Ceriodaphnia*, *Diaphanosoma*) and small calanoid copepods.

Morphology of ephippia

In order to use an identification key based on ephippium morphology, a preliminary introduction to morphological characteristics of ephippia and features diagnostic for the different subgenerea is useful. Figure 2 shows the ultrastructural characteristics of ephippia and diagnostic features needed for identification. Depending on the species and subgenus some characteristics are absent or present on the ephippium.

Ephippia of species belonging to the subgenus *Ctenodaphnia* (except for species formerly belonging to the genus *Daphniopsis*, Hebert, 1995) are characterised by a pair of anterior appendages, each with a row of spines, which are derived from the dorsocephalic suture between the head shield and the carapace (Fig. 2). In most species (subgenera *Hyalodaphnia*, *Daphnia* and some *Ctenodaphnia*) the ephippial capsule reaches the ventral edge of the carapace, at the base of the terminal spine. In other

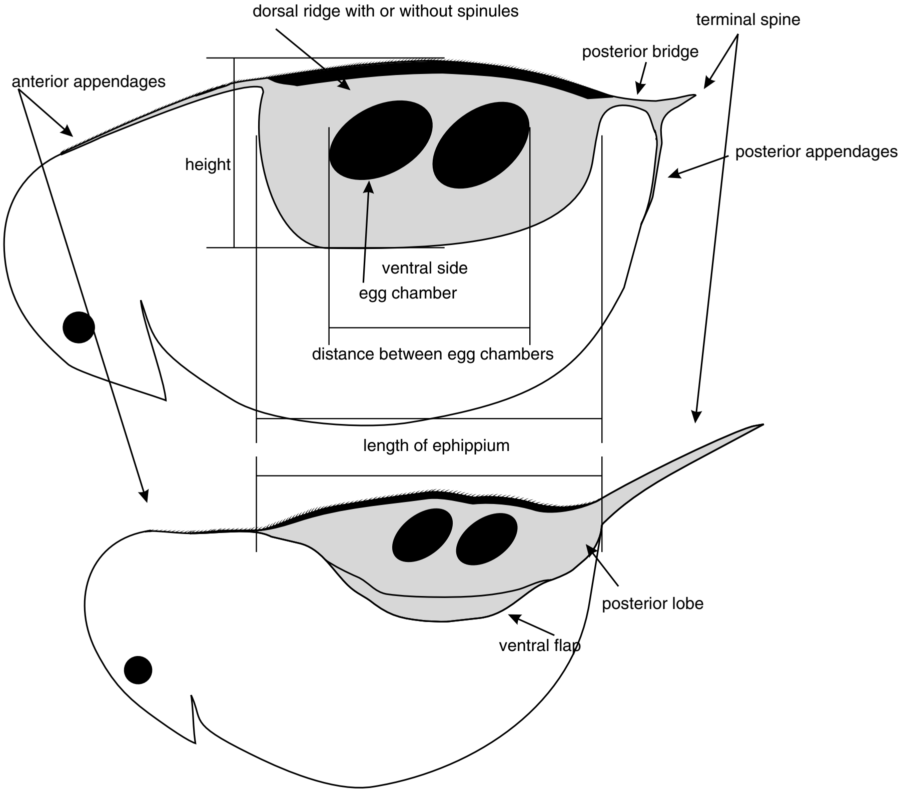

Figure 2. Morphological descriptors of ephippia.

Ctenodaphnia species (e.g., *D. lumholtzi*, *D. magna*, *D. similis*) the ephippial capsule does not reach the edge of the maternal carapace; in these cases the terminal spine of the carapace is connected to the ephippium by a narrow posterior bridge (Fig. 2a), or is not connected at all (e.g., *D. lumholtzi*). In a few species (e.g., *D. magna*) the sclerotised ventro-posterior margin of the maternal carapace is retained after shedding of the ephippium, forming the ventro-posterior appendages (Fig. 2a).ln some species the two valves of the ephippium are always open at the ventral side, forming two ventral flaps standing outward, showing the internal cuticula surrounding the embryos (e.g., *D. barbata*). In these species the ephippium reaches the ventral margin of the maternal carapace (Fig. 2b). In *Ctenodaphnia* the two egg chambers are positioned obliquely relative to the dorsal margin, sometimes almost horizontally. Spinules are always present on the dorsal ridge (except for species formerly belonging to the genus *Daphniopsis*, Hebert, 1995) and are mostly large. At least six *Ctenodaphnia* species are present in equatorial East Africa: *D. barbata*, *D. dolichocephala*, *D. lumholtzi*, *D. magna*, *D.* cf. *similis* and *Daphnia* sp. nov. type Limuru).

Representatives of the subgenus *Hyalodaphnia* mostly have a smooth dorsal ridge. The egg chambers are positioned more or less perpendicularly to the dorsal ridge, but can be tilted a little towards the anterior side as well as the posterior side. The anterio-ventral corner is often bulging out a little beyond the dorsal ridge (Fig. 2d). No appendages are present. The terminal spine is often very long, but breaks off easily. At least three species are present: *D. curvirostris*, *D. longispina s.l.* and *D. laevis*.

Members of the subgenus *Daphnia s.s*, mostly have a dorsal ridge with relatively small but numerous spinules. A few species have, however, a smooth dorsal ridge (Hebert, 1995). The egg chambers are positioned more or less perpendicularly to the dorsal ridge. The anterior side is mostly straight, in some species bulging out like in many *Hyalodaphnia*. Only two species of this subgenus have been found in East Africa: *D. obtusa* Kurz and *D. pulex*.

Identification key to the ephippia of Daphnia *species found in Kenya*

1 (a) Ephippium with anterior appendages, however often broken off in damaged specimens. Egg chambers positioned obliquelyrelative to the dorsal ridge. Dorsal ridge with (large) spinules → 6 *(Ctenodaphnia)*

(b) Ephippium without anterior appendages. Egg chambers positioned more or less perpendicular to the dorsal ridge. Dorsal ridge with or without spinules. If present, relatively small. → 2

2 (a) Dorsal ridge with spinules → 3

(b) Dorsal ridge smooth, without spinules; L/H ratio >1.4 (1.3). Posterior end of ephippium body strongly tapered. The anterior end ften

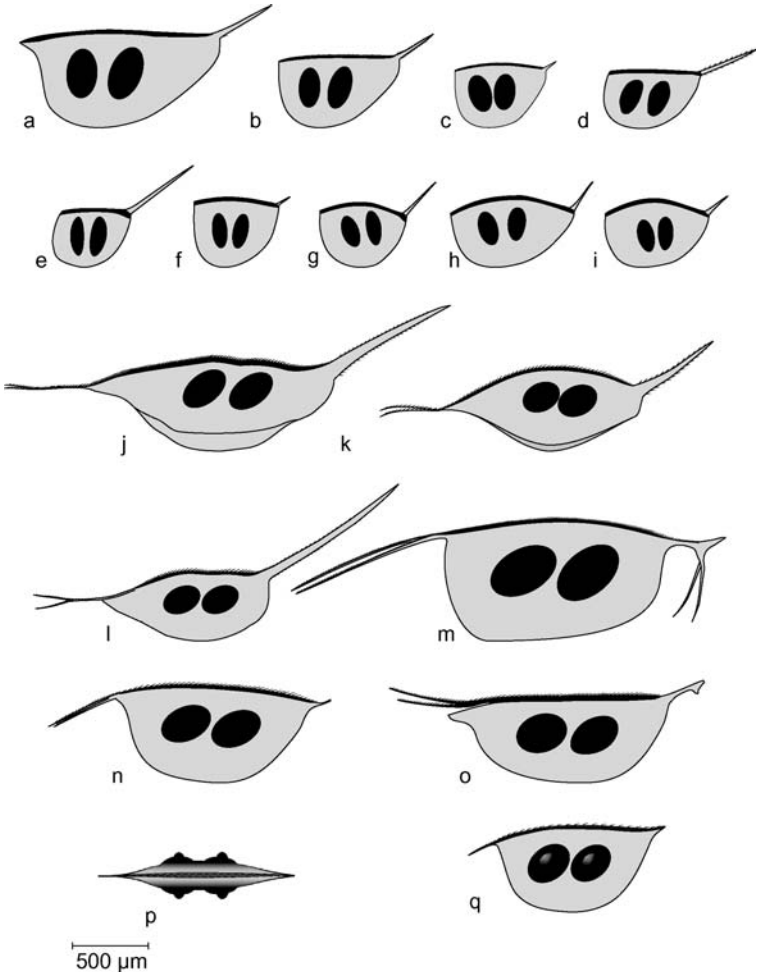

Figure 3. Schematic drawings of ephippia of *Daphnia* species found in Kenya. In brackets the locality from which the individuals originate that were used for the drawings. a, b: *D. pulex* (Lake Naivasha, Kenya); c: *D. obtusa* (Lake Limuru2, Kenya); d: *D. longispina* s.l. (Lake Naivasha, Kenya); e: *D. laevis* (Lake Naivasha, Kenya); f–i: *D. curvirostris,* different morphs. Only morph f found so far in Kenya (Lake Naivasha) (g–i: Czech republic, collection A. Petrusek); j: *Daphnia* sp. nov. (Limuru, Kenya); k: *D.dolichocephala* (Bandasa Lake, Mt Kenya); I: *D. barbata* (Lake Naivasha, Kenya); m: *D. magna* (Lake Naivasha, Kenya); n, o: D. *similis*, different morphs (n: Jordan, collection Prof H. Dumont; o: Germany, collection A. Petrusek); p: *D. lumholtzi*, dorsal view (Lake Naivasha, Kenya); q: *D. lumholtzi* (Lake Naivasha, Kenya).

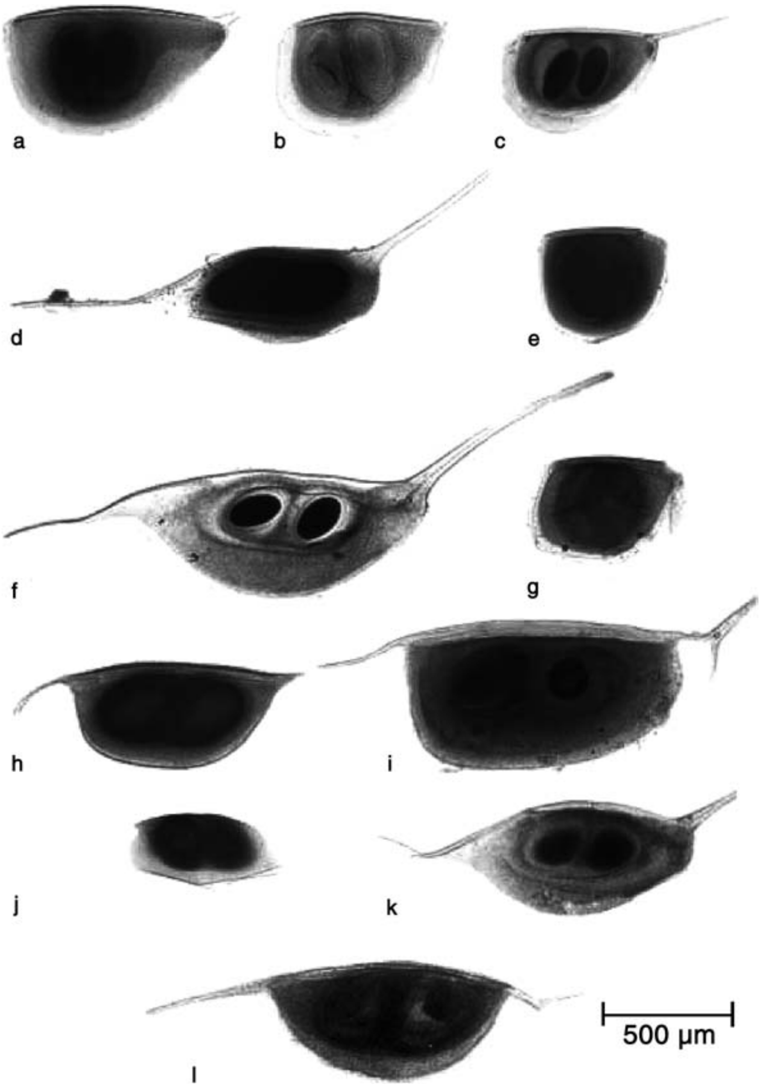

Figure 4. Photographs of ephippia *of Daphnia* species found in Kenya. a: *D*. pu/ex(Lake Naivasha, Kenya); b: *D. obtusa* (Lake Limuru2, Kenya); c: *D. longispina* s.l. (Amboseli swamps, Kenya); d: *D. barbata* (Lake Naivasha, Kenya); e: *D. curvirostris* (Lake Naivasha, Kenya); f: *D.* sp. *nov*. (Limuru, Kenya); g: *D. laevis* (Lake Naivasha, Kenya); h: *D. lumholtzi* (Lake Naivasha, Kenya); i: *D. magna* (Lake Naivasha, Kenya); j: *D. dolichocephala* (Lake Bandasa, Mt Kenya), internal cuticle; k: *D. dolichocephala* (Bandasa Lake, Mt Kenya); I: *D. cf. similis* (Kassala, Sudan, collection H. Dumont).

bulges out a little. → *D. longispina s.l.* (Figs. 3d and 4c).

3 (a) Largest spinules very small, often only visible microscopically (~1–5 μm). Ephippium hardly tapered towards posterior end (terminal spine). → 4

(b) Largest spinules clearly visible at low magnifications (>5 μm), very numerous. Anterior side never bulging out clearly. Ephippium always tapered → 5

4 (a) Anterior side clearly bulging out. Dorsal ridge highest towards posterior end. → *D. laevis* (Figs. 3e and 4g)

(b) Anterior margin never bulging out clearly, perpendicular to dorsal ridge or slightly oblique. Dorsal ridge not higher posteriorly. → *D. curvirostris* (Figs. 3f and 4e)

5 (a) L/H ratio 1.4–2.1, mostly >1.5. Dorsal margin only slightly convex or straight. Very variable in shape and size (0.6–1.7 mm). Dorsal ridge in large ephippia sometimes well extended anteriorly beyond rest of ephippium, making the anterior margin sigmoidal (Fig. 2b). → *D. pulex* (Figs. 3a, b and 4a)

(b) L/H ratio < 1.4. Rather small. Dorsal margin often a little convex, with a twist above the posterior egg chamber. Tapering of posterior end less pronounced than in *D. pulex* (compare Fig. 3b and c), and terminal spine always very short. → *D. obtusa* (Figs. 3c and 4b)

6 (a) Ephippium with small protuberances on both sides of each egg chamber (Fig. 3p). Ephippium without terminal spine; Anterior appendages short (∼/4 of total length of ephippium) and curved downwards. Margin of posterior side elongated and sigmoidal; margin of anterior side sigmoidal; ventral margin rounded. Very few (25–50) but large (20–35 μm) spinules on dorsal ridge. L/H ratio 1.8–2.4. → *D. lumholtzi* (Figs. 3p, q and 4h)

(b) No bumps on lateral side of egg chambers. Anterior appendages longer than 1/4 of total length of ephippium. → 7

7 (a) Ephippium with posterior bridge and terminal spine not directly connected to the ephippium (Fig. 2a). Posterior appendages present or absent → 8

(b) No posterior bridge or posterior appendages present. Terminal spine directly connected to the ephippium (Fig. 2b). Ephippium elongated, anterior side tapered, posterior side with a lobe → 9

8 (a) Posterior appendages present. Very large, 1.0–1.7 mm. Rectangular shape, but greatest height nearly always at anterior end. L/H ratio 1.6–2.0. Dorsal ridge straight or slightly convex, very densely spined (>80 spinules per row). → *D. magna* (Figs. 3m and 4i)

(b) Ephippium without posterior appendages, always broken off at the base of the terminal spine near the bridge. Large to very large (0.9–1.5 mm). Greatest height mostly in the middle or near the posterior end of the ephippium. L/H ratio (1.9) 2–2.4. Dorsal margin with large spinules, < 80 per row. Anterior side sigmoidal, posterior side elongated sigmoidal. ventral side clearly rounded, ephippium not with rectangular shape, the top of the anterior side is often detached from the dorsal margin (Fig. 3o) → *D. similis* (Figs. 3n, o and 4l)

9 (a) Dorsal side of inner cuticle surrounding embryos convex and without depression between eggs, ventral side more or less straight (Fig. 4j). Dorsal ridge of ephippium clearly curved and convex. Large spines on dorsal margin, < 60 per row. Large ventral flaps present (20–35% of total heigth). ventro-anterior margin well defined (compare with *D. barbata*); L/H ratio 2.2–2.7 → *D. dolichocephala* (Figs. 3k and 4j, k) (in some cases *D. barbata* has a straight or slightly convex dorsal margin, without depression; check ventro-anterior margin and size of ventral flaps).

(b) Dorsal margin undulated due to depression between egg chambers, sometimes only very slightly, in rare cases straight or slightly convex. Inner cuticle surrounding embryos with strong depression between eggs (Fig. 4f) → 10

10 (a) Dorsal margin with very large (40–60 μm) but relatively few spines (20–60 per row). Ventro-anterior margin ill defined beyond the anteriormost egg chamber, very thin and translucent, often damaged (Figs. 3l and 4d). Ratio L/H 2–2.4. Ratio L/(total length of egg chambers) 1.5–2. Ventral flaps not so large, max. 25% of total height (mostly < 15–20%). total length of ephippium 0.6–1.1 mm → *D.* banbafa (Fig. 3l)

(b) Dorsal margin with 50–80 spines per row, mostly smaller than those of *D. barbata* (30–50 μm). ventro-anterior margin clearly defined, not thinner than other parts of ephippium (Fig. 4f). Anterior side elongated sigmoidal. Ratio L/H 2.4–2.7. Ratio L/(total length of egg chambers) 2–2.7. Ventral flaps very large, easily 30% of total heigth and often standing outwards (Fig. 4f). total size 1–1.6 (1.8) mm. → *D. nr. gibba* (Figs. 3j and 4f)

Discussion

Taxonomic considerations

Due to the recent accumulated knowledge of genetic relationships within the genus *Daphnia,* the taxonomy of this genus is not fully stabilised. One is often dealing with groups of sibling species, without consideration of the relationships with members of the type population. This is the case for many species considered in this paper, like *D. obtusa*, which is thought to consist of more than 12 sibling species worldwide (Hebert & Finston, 1996; Adamowicz et al., 2004; A. Petrusek, personal communication; V. Korinek, perssonal communication). Unless mentioned otherwise, identification in the key is solely based on Kenyan populations. Identification of *Daphnia obtusa* in this paper was based on Belgian populations because only one ephippium from Kenya was found, and no African populations were available. Daphnia *laevis* equally consists of more than four sibling species (Taylor et al., 1996; Adamowicz et al., 2004) while the African *D. laevis* is morphologically and genetically distinctive from American siblings (J. Mergeay, unpublished results). *Daphnia lumholtzi* also consists of a complex of at least two but probably four sibling species (Havel et al., 2000; Korinek, personal communication). Equally, *Daphnia pulex* consists of genetically very distinct sibling species (Colbourne et al., 1998), while *D. similis* is made up of at least three and probably five sibling species (A. Petrusek, personal communication). Identification of ephippia of *D. similis* was based on ephippia from Jordan (collection H. Dumont) and Germany (collection A. Petrusek). Regarding the species group of *D. hyalina*, *D. galeata*, *D. longispina* and *D.* rosea, which were all previously recorded in East-Africa (Lowndes, 1936; Green, 1995; Schwenk et al., 2000), a lot of confusion exists regarding the exact identity of these species (e.g. Schwenk et al., 2000). They are therefore recorded here as *D. longispina s.l.*

Given the uncertain taxonomic status of the sibling species mentioned above, we must stress that many of the species considered are in fact different from the sibling species from the type locality, or have an uncertain taxonomic relationship with specimens from the type locality.

The presence of Daphnia *in the active vs. dormant community*

More than twice as many species were found in the dormant community compared to the active community. This is consistent with other studies that assessed both the active and the dormant community (May, 1986; Havel et al., 2000; Vandekerkhove et al., submitted), confirming that species are easily overlooked when only the active community is sampled. Identification of dormant specimens is possible by hatching them and culturing them until the active specimens can be identified (Vandekerkhove et al., submitted), but this approach is time-consuming and elaborate. Identification of ephippia based on morphology, on the other hand, is fast and can also be practiced on damaged or unviable ephippia (Vandekerkhove et al., submitted). In case of doubt, hatching and identification of adults can still be done. Moreover, modern genetic techniques allow accurate species assignments based on minute amounts of DNA, and can be used to confirm morphological identifications (e.g., Duffy et al., 2000).

In all but one of the studied water bodies in which *Daphnia* was found in the active community, the same species were also found in the dormant community. This indicates that sexual reproduction readily occurs in equatorial East Africa and that the dormant community actually represents the species found in the active community. In a few situations, however, sexual reproduction is very rare; in Lake Victoria, e.g., ephippia of *Daphnia are* rarely found in the sediment (D. Verschuren, personal observation), yet at least three species are present (Jonna & Lehman, 2002). This is probably due to the state of ‘endless summer’ which prevails in such stable tropical lakes that are hardly influenced by seasonal changes (Kilham & Kilham, 1990; Lehman, 1996). It is therefore advised to sample both the dormant and the active community.

In many of the studied water bodies, *Daphnia* were very scarce, in the active as well as in the dormant community, with only a few individuals per sample. On the other hand, *Daphnia* was found in a high number of water bodies (~70%). A few lakes had four or more species of *Daphnia.* The sediment record of Lake Naivasha even shows that at least eight species have been present in Lake Naivasha since 1900 AD (Mergeay et al., submitted), indicating that dispersal is probably not the most important limitation. Most water bodies studied in which *Daphnia* were present, however, contained only 1–2 species.

Geographic distribution of Daphnia *species and ecological considerations*

Three species of *Daphnia* are considered typical for tropical African lowlands: *D. barbata*, *D. laevis* and *D. lumholtzi*, *D. laevis* and *D. barbata are* both widespread in sub-Saharan Africa but are absent from the central African tropical rainforests (Dumont, 1979; Green & Kling, 1988; Green, 1990; Egborge et al., 1994, Hart, 1999, 2001;). *D. barbata* is also found in the Nile system and a few North African water bodies (Dumont, 1979). *D. barbata* is ubiquitous in turbid and productive water bodies, with conductivities ranging from <100 μS cm^{-1} to at least 5000 μS cm^{-1} (Mergeay et al., in preparation). *D. laevis* is typically found in relatively clear water bodies, but can also occur in more turbid systems (Secchi depth 0.4 m). Conductivity tolerance of *D. laevis* is probably less than 1000 μS cm^{-1}. *D. lumholtzi* is typically found in large lakes (Victoria, Albert, Edward, Naivasha, Tchad & Green, 1967; Dumont, 1979) in tropical Africa. It is common throughout the Nile basin (Sudan, Egypt), being found in ponds as well as in rivers (Dumont, 1979; Elhigzi et al., 1995). It is further distributed in Australia, South-Asia and Eastern Europe (Dumont, 1979), and was recently introduced in North America (Havel & Hebert, 1993). The Australian populations are however genetically significantly different from Asian and African populations (Havel et al., 2000). *D. lumholtzi* can withstand relatively high turbidity levels (Work & Gophen, 1999), but probably not as high as the levels *D. barbata* can tolerate. Just like *D. barbata* it can grow at temperatures up to 30 °C (Work & Gophen, 1999). *D. dolichocephala* is a rare and poorly known species. Up to now it has, in tropical Africa, only been found in water bodies on Mt. Kenya (Löffler, 1968). In the same water bodies, we found ephippia most probably belonging to this species. It is further found in southern Africa (Sars, 1895; Green, 1995), and is probably endemic to Africa. The relations between the different populations on the African continent (Kenyan vs. South-African) are however uncertain (V. Korinek, personal communication). *D. magna* is a typical temperate species that has a mainly Holarctic distribution (Hebert, 1995), but is also present in numerous North African temporary water bodies (Dumont, 1979). It is rather rare in East Africa but is yet found in a variety of habitats, ranging from alpine lakes on Mt. Kilimanjaro (Löffler, 1968) to large (eutrophic) lakes (Lake Naivasha, Lake Victoria, Lake Ol Bolossat) and eutrophic ponds with sewage waste water in Nairobi (B. Riddoch, personal communication). *D. magna* can be expected to be found more in southern Africa as well, as suggested by its presence in Botswana (B. Riddoch, personal communication). Competition with other species better adapted to high temperatures and high turbidity levels may however limit its distribution. *D. cf. similis* was found only once in Lake Oloidien in the 1990s as a single ephippium (D. Verschuren, personal observation). Its range in tropical Africa is poorly known. It is, however, common in the hydrological basin of the Sahara and Sahel, but is less resistant to high salinity levels than *D. magna* (Dumont, 1979). *D. pulex* is a nearly cosmopolitan species, but consists in fact of a species complex of which the internal boundaries are not yet completely known (Colbourne et al., 1998). It is uncommon in tropical Africa, occurring from 900 m a.s.l. (Lake Baringo) up to more than 3000 m (Green, 1995). Its range in Africa is not completely known, but its common occurrence in southern Africa (Green, 1995; Hart, 2001) and Zimbabwe (Green, 1990) suggests it may be widespread in permanent water bodies in subtropical regions and at higher latitudes and altitudes. *D. pulex* is found at conductivities up to 1000–1500 μS cm^{-1} and also withstands relatively high turbidity levels, given its common presence in Lake Naivasha today (Secchi depth ca. 25 cm in January 2003). It was also present at low densities in a sediment sample from Lake Baringo in 2001, but it was absent in sediment samples taken in 2003. The current turbidity and conductivity levels in Lake Baringo (Secchi depth <5 cm; conductivity 1500–2000 μS cm^{-1}) may have caused the extinction of this species. D. *curvirostris* is a typical temperate species. In this study it was only found in two high-altitude clear lakes. It was present in

Lake Naivasha, however, at least between 1940 and 1955 (Mergeay et al., submitted). Apart from East Africa (Green, 1965, 1995) it has a mainly Holarctic distribution, occurring throughout Eurasia as well as northwestern Canada (Duffy et al., 2000). In tropical Africa it seems restricted to high altitudes (1800–4000 m; Green, 1995).

Direct and indirect effects of temperature are probably key factors limiting the distribution of *D. curvirostris* in the tropics. In our samples only one morphotype of *D. curvirostris* was found (Fig. 3f). There are, however, several very different morphs, more resembling *D. obtusa*, occurring in Europe. They might be found in Africa as well, and are represented in Figs 3g and h. *D. obtusa* was found only once during this study at an altitude of approx. 2300 m, but was previously recorded on Mt. Kenya and in the Ruwenzori mountain range (Uganda) at high altitudes (Löffler, 1968). Other members of this species complex are found in the Holarctic, Southern African and South-America. *D. longispina s.l.* was found only once in this study, in a relatively cool (20 °C) water body with abundant submerged and emergent vegetation, but only in the resting egg bank (Table 1). It was, however previously found in the sediment record of Lake Naivasha (Mergeay et al., submitted), as well as in a high altitude lake in the Ruwenzori range (J. Mergeay, personal observation.). It has further been found in a number of large East African lakes (Lake Victoria, Lake Edward and Lake Chad, and in Lake Tana, Ethiopia as *D. hyalina;* Green, 1965, 1995; Dumont, 1979; Schwenk et al., 2000; Jonna & Lehman, 2002). *Daphnia* sp. nov. type Limuru is a new species of *Ctenodaphnia* (V. Kořinek, personal communication). It was found in four water bodies in the active as well as the dormant community, at altitudes above 2200 m a.s.l. Additionally there are two isolated historical records of its presence in Lake Naivasha (~1900 m a.s.l.) (Mergeay et al., submitted). Except for one case, the water bodies in which this species was found were very turbid. In conclusion, the *Daphnia* fauna of Equatorial East Africa apparently is *a* mixture of typical African species (*D. laevis*, *D. barbata*, *D. lumholtzi*, *D. dolichocephala*, *D.* sp. nov. type Limuru), nearly cosmopolitan species (*D. pulex*) and Holarctic/Palearctic species that are restricted in the tropics to cold refugia at higher altitudes (*D. curvirostris, D. obtusa* species complex, *D. longispina s.l.*, *D. magna*).

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