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Article



Nothobranchius kadleci (Cyprinodontiformes: Nothobranchiidae), a new species of annual killifish from central Mozambique

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Abstract

Nothobranchius kadleci, a new African annual killifish species, is described from the drainages of the Save, Gorongose, Pungwe and Zangue Rivers in the Sofala Province of central Mozambique. Nothobranchius kadleci is similar to Nothobranchius furzeri from which it is distinguished by colouration (red pelvic fins, red lips, more extensive red colouration on body) and morphology (larger distance between pectoral and pelvic fins, shorter anal and dorsal fins, and shorter base of the anal fin). The currently known distribution of these two species is allopatric, with the *N. kadleci* range north of the *N. furzeri* range. Nothobranchius kadleci occurs sympatrically with Nothobranchius orthonotus and Nothobranchius rachovii, from which it can clearly be distinguished by different colour patterns of the fins and body, head shape and morphometric characteristics. A total of 12 populations were recorded between the northern bank of the Save River and southern bank of the Zambezi during collection trips in February 2008 and February 2009.

Key words: Save River, Beira region, Sofala Province, Zambezi, Limpopo

Introduction

The genus *Nothobranchius* (Cyprinodontiformes: Nothobranchiidae) is comprised of small (3–15 cm), shortliving (3–12 months) fish inhabiting temporary habitats such as isolated savannah pools throughout eastern Africa, from southern Sudan to KwaZulu-Natal in South Africa. The genus currently includes at least 50 valid species, separated into five subgenera (Huber 2000; Wildekamp 2004). All *Nothobranchius* species are annual. They hatch at the start of rainy season and sexually mature within a few weeks. After reaching sexual maturity, they reproduce daily and females lay 5–50 eggs/day (Haas 1976a). Eggs remain in the substrate after pools desiccate and survive in developmental diapause until the next rainy season (Wildekamp 2004). *Nothobranchius* species are sexually dimorphic and dichromatic; males are robust and colourful while females are pale. The bright male colouration is sexually selected (Haas 1976b) and species specific (Huber 2000). Many species occur in several colour forms that may be either sympatric or allopatric (Huber 2000; Wildekamp 2004; Reichard *et al.* 2009). Several *Nothobranchius* species may co-occur in sympatry in the same pool (Huber 2000).

At least five *Nothobranchius* species are reported from Mozambique (Woods 2000; Skelton 2001; Wildekamp 2004; Valdesalici 2007; Valdesalici & Hengstler 2008; Reichard *et al.* 2009; Watters et al. 2009). The distribution of *Nothobranchius furzeri* Jubb, 1971 is restricted to southern Mozambique, with records from basins of the Limpopo and Incomati Rivers (Jubb 1971; Wood 2000; Terzibasi et al. 2008; Watters *et al.* 2009; reviewed in Reichard *et al.* 2009). The range of *Nothobranchius orthonotus* (Peters, 1844) extends from KwaZulu-Natal in South Africa in the south to the northern banks of the Zambezi River in Quelimane in the north (Wildekamp 2004). Two closely related species, *Nothobranchius kuhntae* (Ahl, 1926) and *Nothobranchius mayeri* Ahl, 1935, both often synonymised with *N. orthonotus* (Wildekamp 2004), were described from Beira region in central Mozambique (Ahl 1935; Ahl 1936). *Nothobranchius rachovii* Ahl,

1936 ranges from Kruger National Park in South Africa to Quelimane (north of the lower Zambezi) and likely consists of three separate species differing in the number of chromosomes and being separated by the Save and Zambezi Rivers (Watters *et al.* 2009). Finally, two new species from the *Nothobranchius melanospilus* species group (Wildekamp 2004), *Nothobranchius hengstleri* Valdesalici, 2007 and *Nothobranchius krammeri* Valdesalici & Hengstler, 2008, were recently described from northern Mozambique, with at least one additional species from the same complex awaiting formal description (Valdesalici 2007; Valdesalici & Hengstler 2008).

A new species of *Nothobranchius* from central Mozambique is reported here. It has been recorded during extensive survey of *Nothobranchius* populations in southern and central Mozambique during a field expedition of the Czech Academy of Sciences in February 2008 and 2009. The new species was recorded in 12 isolated pools between the northern bank of the Save River and the Zambezi River.

Materials and methods

Fish were collected using a dipnet and preserved in 4 % formaldehyde solution immediately after capture. Morphological measurements (to the nearest 0.1 mm) and meristic counts were taken according to Holčík (1989), partially under a dissecting microscope. Morphometric data are presented as percentage of standard length (SL), measured from the tip of snout to the posterior end of the hypural plate, except for traits related to head morphology that were expressed as percentage of head length, measured from the tip of snout to the distalmost extent of operculum. The number of scales in a longitudinal row was counted along the lateral line, excluding scales on head and posterior of hypural plate (Holčík 1989). Type material is deposited in Museum für Naturkunde, Berlin, Germany (ZMB), Royal Museum for Central Africa, Tervuren, Belgium (MRAC) and National Museum, Prague, Czech Republic (NMP). A comparison was additionally made with material deposited in Albany Museum, Grahamstown, South Africa (AMG) and material collected during expeditions of the Institute of Vertebrate Biology, Czech Academy of Sciences, Brno, Czech Republic (MZCS).

Comparative material examined

Nothobranchius furzeri Jubb, 1971

Type material: holotype AMG PF1239, male, 44 mm SL, Sazale Pan, GonaReZhou, Zimbabwe, 21° 40' S, 31° 45' E.

Other specimens: population MZCS-08/2, lower Limpopo Basin, Gaza Province, Mozambique, 24° 03.8' S, 32° 43.9 E: ZMB 33912, male; ZMB 33913, female; MRAC 2009-12-P-3, male; MRAC 2009-12-P-4, female; NMP P6V 86689, male; NMP P6V 86690 (female). Population MZCS-08/124, 7 males, Vaneteze River basin, Gaza Province, Mozambique, 24° 35.6' S, 32° 24.3' E.

Nothobranchius orthonotus (Peters, 1844)

Type material: lectotype ZMB 4754 (Quelimane, Mozambique); paralectotypes ZMB 6873, 5 specimens; paralectotypes ZMB 21481, 10 specimens; *Nothobranchius kuhntae* (Ahl, 1926) lectotype ZMB 21479, male, Beira, Mozambique; *N. kuhntae* paralectotype ZMB 21477, 1 specimen; *N. kuhntae* paralectotypes ZMB 21480, male and female; *Nothobranchius mayeri* holotype ZMB 21155, male, Beira, Mozambique.

Other specimens: MZCS-08/107, male, Save River basin (northern bank), Sofala Province, Mozambique, 21° 00.9' S, 34° 27.89' E.

Nothobranchius rachovii Ahl, 1936

Non-type specimens: MZCS-08/100, 5 males, Buzi River Basin, Sofala Province, Mozambique, 19° 58.6' S, E 34° 09.9' E; MZCS-08/104, 2 females, Buzi River Basin, Sofala Province, Mozambique, 19° 56.9' S, 34°

10.1' E; MZCS-08/113, male and female, Save River Basin (southern bank), Gaza Province, Mozambique, 21° 12.0' S, 34° 43.6' E.

Nothobranchius kadleci, new species

Figs. 1 & 2, Table 1

Holotype. ZMB 33909, male, 38.1 mm SL, Sofala Province, Mozambique, temporary pool about 100 m from the main EN1 national road, not connected to any permanent river system, 20° 41.3' S, 34° 06. 4' E (collection code MZCS 08/91), collected by Martin Reichard, Matej Polačik, Ondřej Sedláček, 18 February 2008.

Paratypes. ZMB 33910, female, 32.2 mm SL; MRAC 2009-12-P-1, male, 40.2 mm SL; MRAC 2009-12-P-2, female, 35.8 mm SL; NMP P6V 86687, male, 36.1 mm SL; NMP P6V 86688, female, 31.0 mm SL. All paratypes share same collection data as holotype.

Non-type material. MZCS-08/99, 3 males and 3 females, Pungwe River Basin, Sofala Province, Mozambique, 19° 17.4' S, 34° 13.8' E; MZCS-08/107, 5 males, border of Save and Gorongose River Basins, Sofala Province, Mozambique, 21° 00.9' S, 34° 27.8' E.

Diagnosis. Nothobranchius kadleci is distinguished from N. furzeri by the smaller depth of the dorsal fin (17.9–31.0 % SL vs. 27.4–37.7 % SL in N. furzeri in males, 14.9–17.6 % SL vs. 19.0–21.9 % SL in females) and smaller depth of the anal fin (17.4–25.8 % SL vs. 22.4–32.4 % SL in N. furzeri in males, 17.3–19.2 % SL vs. 19.3–24.5 % SL in females), larger preanal distance (64.0–65.8 % SL vs. 58.9–61.3 % SL in N. furzeri) in females and presence of red colour on gill membrane and lips and red pectoral fins (N. furzeri does not possess red colour on gill membrane and lips and typically have yellow pectoral fins), absence of black marginal band on caudal fin (present in some male N. furzeri), and a higher amount of red on caudal and dorsal fins and on body in males.

It is distinguished from sympatric *N. orthonotus* (including putative *N. kuhntae* and *N. mayeri*) by the shape of the frontal region (convex in *N. kadleci*, flat in *N. orthonotus*), the presence of red pectoral fins with white margins, often with a bluish tint (*N. orthonotus* possess transparent or whitish pectoral fins with red margins), red background colour on the head covered with small to large light blue marking (*N. orthonotus* possess red spots on white to grey background colour of the head and, in most populations, also on anterior ventral part of the body), shorter preanal distance (range 58.4–61.2 % SL vs. 62.7–72.5 % SL in *N. orthonotus*), and distance between pelvic and anal fins (10.2–13.5 % SL vs. 13.4–16.6 % SL) in males.

Nothobranchius kadleci differs from sympatric *N. rachovii* in males by a lack of black margin of the caudal fin, distance between pectoral and pelvic fins (15.1–21.7 % SL vs. 12.8–16.7 % SL in *N. rachovii*), minimal body depth (15.0–16.9 % SL vs. 13.5–15.4 % SL) and eye diameter (22.1–27.3 % HL vs. 26.0–32.6 % HL) and in females by preanal distance (64.0–65.8 % SL vs. 61.8–64.5 % SL), length of caudal peduncle (20.1–21.6 % SL vs. 13.4–20.1 % SL), depth of dorsal fin (14.9–17.6 % SL vs. 16.8–23.2 % SL), and depth of anal fin (17.3–19.2 % SL vs. 21.0–23.2 % SL).

Description. Morphology and general body shape similar to *N. furzeri* (Figs. 1 & 2, Table 1). A robust *Nothobranchius* species with a characteristic convex frontal region, in mature males sometimes exaggerated into a distinctive frontal hump. The dorsal fin 13–14 rays, anal fin 13–14 rays (up to 16 in females), pelvic fin 6 rays and pectoral fin 16–18 rays. In males, pectoral fins typically overlap with pelvic fins (50 % of the pectoral fin is beyond the anterior margin of pelvic fin). Pelvic fins reach or slightly overlap the base of the anal fin. The longest rays of dorsal and anal fins reach or extend beyond the anterior margin of the caudal fin. In females, the longest rays of the pelvic fin just reach the anal fin base. About 30 % of the pectoral fin extends beyond the base of the pelvic fin. The tip of female anal fin does not reach the caudal fin, but the dorsal fin sometimes reaches the caudal fin. The longitudinal series possesses 27–29 scales; one large male (50.2 mm SL) with 34 scales in the longitudinal series was recorded.



FIGURE 1. A. *Nothobranchius kadleci*, holotype, adult male, 38.5 mm SL, ZMB 33909 (upper fish) and paratype, adult female, 32.8 mm SL, ZMB 33910 (lower fish) from Mozambique, Sofala Province, isolated savannah pool in the Gorongose River drainage, stored in 4 % formaldehyde for one year. B. Adult male N. kadleci with a frontal bump (upper fish) and sympatric *N. orthonotus* male (lower fish). Note the difference in head and body shape.



FIGURE 2. Adult males of *N. kadleci* photographed in the wild (A–C) and in aquarium 1–2 months after capture (D–F). Males are either of red form (left panel) or blue form (right panel). Note a distinct frontal hump on male pictured at photograph (C). Individual on panel (D) is a subadult and has yet not fully developed colouration. Panels (A) and (E) show the same individual in the field and in aquarium. Photos by O. Sedláček (A, B, D, E & F), and R. Blažek (C).

Live colouration. Males. Colouration varies from deep red to light blue and appears to be continuous rather than falling into two discrete colour forms (Figs. 2 & 3). Fully red males have an entirely red caudal fin. The dorsal fin is red with a narrow white margin and white (over the entire fin) or yellow (in the anterior 1/3 of the fin) irregular dots and lines on the fin membrane. The anal fin is red with a narrow white margin and white dots or lines, though white marking is less developed than in the dorsal fin. Pectoral fins are red with white or light blue tips. Ventral fins are red, sometimes with traces of white marking. The body is red, including the head, lips and gill membrane. Scales have large light blue centres, giving an impression of a reticulated pattern on the entire body. In blue males, the base colour of the fins is also red, but light blue (or sometimes whitish) dots and lines are abundant on all fins except for the pectoral fins (which are always red in

wild, sexually mature males, though red colour may be less developed in subadult males). In blue males, especially subadult specimens, light blue marking on the body covers a large extent of the red, including a large area of the head. The eyes of all males are orange to gold with a dark vertical band.



FIGURE 3. Comparison of adult *N. kadleci* with related species; (A) male *N. kadleci* (left) with allopatric male *N. orthonotus* from Beira region (right), (B) female *N. kadleci* (lower) with sympatric female *N. orthonotus* (upper), (C) male *N. kadleci* (lower) with sympatric male *N. orthonotus* (upper) and (D) male *N. rachovii*, a species sympatric with *N. kadleci*. Allopatric *N. furzeri* male of (E) red form and (F) yellow form. Photos by O. Sedláček.

Females. All fins are transparent. A slight yellowish tint may be present on the distal part of the dorsal and anal fins. The body is light yellow to light brown, with the posterior part of scales shining an iridescent light blue. Sometimes (<10 % of specimens), small black dots appear on the body. The eye is orange to gold, with a black vertical band.

Colouration in preservative. After one year of preservation in 4 % formaldehyde solution, male colouration was yellow to light brown (similar to live colouration of females), and the pelvic part whitish (Fig. 1A). Black marking is present on the opercular region, gill membrane and distal part of dorsal fin of some

individuals (including the holotype). Small black dots are present on the caudal and dorsal fins. The anal, pelvic and pectoral fins are orange. Female body colouration is identical and fins are transparent. Rarely, the black dots are visible.

TABLE 1. Morphometric measurements of *N. kadleci* and *N. furzeri*. Standard length and head length are given, with other variables expressed as a percentage of standard and head lengths, respectively. Measurements taken on male *N. kadleci* (including holotype for which the value is given separately) and male *N. furzeri* were tested using a *t*-test. Characters that were significantly different between *N. kadleci* and *N. furzeri* (P < 0.05) are marked by an asterisk.

		Males					Females				
	Holotype	N. kadi	N. kadleci (N=10)		N. furzeri (N=10)		N. kadleci (N=3)		N. furzeri (N=3)		
SL (mm)	38.5	43.3	38.5	-50.2	43.1	36.1	-47.5	31.3	-34.6	31.0	-35.8
In % of standard length											
total length	121.8	124.2	120.3	-127.9	123.7	119.7	-128.2	121.7	-124.1	119.9	-123.9
head length	34.5	33.8	31.7	-36.2	34.7	31.4	-37.7	29.4	-33.2	31.8	-34.5
predorsal distance	56.4	59.7	56.1	-61.7	60.4	57.3	-63.2	59.7	-62.8	59.5	-62.6
preanal distance	60.3	59.7	58.4	-61.2	59.9	57.3	-61.9	64.0	-65.8	58.9	-61.3
preventral distance	49.9	50.1	46.7	-63.8	48.3	47.1	-51.2	46.6	-52.7	45.8	-48.4
pectoral-pelvic distance*	15.1	16.9	15.1	-21.7	15.0	13.7	-17.7	15.9	-20.7	16.5	-18.7
pectoral-ventral distance	12.2	11.6	10.2	-13.5	12.2	11.2	-13.4	13.6	-16.0	12.3	-21.6
length of anal fin base*	21.8	20.8	18.1	-23.0	22.3	19.7	-24.8	0.0	-19.4	17.1	-19.3
length of dorsal fin base	25.5	25.3	22.5	-27.2	26.0	23.9	-28.0	17.9	-24.9	23.6	-24.9
maximum body depth	28.6	30.0	27.1	-31.9	29.1	26.9	-31.0	23.3	-29.8	23.6	-25.8
depth of caudal peduncle	15.1	16.4	15.1	-17.1	16.3	13.7	-21.5	14.1	-14.9	14.2	-16.1
length of caudal peduncle	16.1	20.1	16.1	-23.7	17.9	13.0	-21.1	20.1	-21.6	0.0	-22.6
minimum body depth	15.1	15.9	15.0	-16.9	15.3	13.7	-16.5	13.1	-14.0	12.6	-13.7
length of caudal fin	21.3	23.0	19.5	-27.1	22.7	18.4	-25.1	22.0	-23.1	19.0	-21.3
depth of dorsal fin*	17.9	25.5	17.9	-31.0	30.8	27.4	-37.7	14.9	-17.6	19.0	-21.9
depth of anal fin *	17.4	21.4	17.4	-25.8	25.7	22.4	-32.4	17.3	-19.2	19.3	-24.5
Head length (mm)	13.3	14.6	13.0	-17.2	15.9	13.0	-26.5	9.2	-11.3	10.7	-11.4
In % of head length											
preorbital distance	26.3	27.7	21.2	-32.6	26.5	23.8	-29.6	22.9	-26.1	19.6	-23.7
postorbital distance	48.9	51.4	47.7	-55.4	52.2	47.3	-58.7	50.0	-52.3	46.7	-47.4
eye diameter	23.3	24.5	22.1	-27.3	26.3	21.4	-58.0	23.9	-29.3	26.2	-28.1
interorbital distance	43.6	47.2	43.6	-52.4	47.2	44.1	-53.2	43.1	-51.1	37.4	-49.1
head depth	78.2	85.5	78.2	-102.1	80.1	71.5	-87.9	76.1	-87.0	69.2	-78.1

Distribution. This new species was found in 12 populations from a relatively large area in central Mozambique, north of the Save River, including the basin of the Save, Gorongose, Pungwe and Zangue Rivers (Fig. 4, Table 2). The altitude of collections sites ranged from 24–82 m above sea level. The latitudinal extent of the range of *N. kadleci* is over 300 km primarily along the north-south axis.

Habitats. All populations of *N. kadleci* were found in small temporary pools varying from $3.5-2150 \text{ m}^2$, with a maximum depth of 10–70 cm in 2008 and 50–100 cm in 2009, very turbid water and soft muddy bottom (Fig. 5, Table 2). Littoral vegetation was present in 50 % of the pools, with scarce *Nymphaea* sp. vegetation in two pools. Conductivity ranged from 68–300 μ S.cm⁻² and water temperature during collection was 27.7–38.2 °C. Sympatric fish species included *N. orthonotus* (10 cases), *N. rachovii* (2 cases), an unidentified small *Barbus* sp. (2 cases), *Tilapia* sp. (1 case), *Protopterus* sp. (1 case) and *Clarias gariepinus* (1 case).



FIGURE 4. Distribution of *N. kadleci* and *N. furzeri*. Populations recorded in February 2008 and February 2009 are denoted, with type localities encircled. Some marks may represent several adjacent populations. Type locality of *N. furzeri* according to Jubb (1971).



FIGURE 5. Habitat of *N. kadleci*; (A) type locality MZCS-08/91 (Gorongose River basin), (B) MZCS-08/107 (Save River basin) and (C) MZCS-08/99 (Pungwe River basin), all sites in central Mozambique, Sofala Province. Photos by O. Sedláček.

Etymology. The species is named in honour of the late Jaroslav Kadlec (1951–2006) from Brno, Czech Republic, a renowned killifish breeder recognized worldwide for his articles on killifish breeding, ecology, and his photographs. To be pronounced "khadlatsi".

TABLE 2. Geographic coordinates and habitat characteristics of 12 sites with <i>N. kadleci</i> researched during the 2008 and
2009 MZCS expeditions.

	Latitude		Longitude		Altitude (masl)	Conductivity $(\mu S \ . \ cm^{-2})$	Temperature (°C)	Max. depth (cm)	Sympatric species	
MZCS 08/91*	20°	41.3' S	34°	06.4' E	62	300	38.2	10		
MZCS 08/92	19°	19.6' S	34°	18.5' E	24	173	33.5	50		
MZCS 08/99	19°	17.4' S	34°	13.8' E	47	220	33.5	75	N. orthonotus, Clarias gariepinus, Barbus sp.	
MZCS 08/107	21°	00.9' S	34°	27.8' E	79	77	30	25	N. orthonotus	
MZCS 08/108	21°	00.7' S	34°	32.2' E	73	100	32.6	50	N. orthonotus, N. rachovii	
MZCS 08/109	21°	00.4' S	34°	32.4' E	82	91	33	25	N. orthonotus	
MZCS 08/110	20°	59.9' S	34°	35.3' E	68	97	34	30	N. orthonotus	
MZCS 08/112	21°	01.7' S	34°	44.7' E	28	109	33.1	40	N. orthonotus	
MZCS 09/40	18°	06.2' S	34°	43.8' E	82	250	28.5	50	N. orthonotus	
MZCS 09/62	18°	08.0' S	35°	01.4' E	39	199	27.7	80	N. orthonotus	
MZCS 09/67	20°	44.4' S	34°	08.7' E	58	68	29	90	N. orthonotus	
MZCS 09/68	20°	44.4' S	34°	08.7' E	58	99	28.9	100	N. orthonotus, N. rachovii, Barbus sp., Tilapia sp., Protopterus sp.	

*type locality.

Discussion

The external morphology of *Nothobranchius kadleci* is similar to that of *N. furzeri*, but the two species clearly differ in their colouration (Figs. 2 & 3) and have apparently allopatric distribution. Many *Nothobranchius* species, including *N. furzeri*, occur in two distinct colour morphs. In other *Nothobranchius* species, more continuous colour variation is found (Wildekamp 2004). This appears to be the case in *N. kadleci*, with a continuous variation from fully red males with some light blue markings on body and fins to males with a larger extent of blue on their body and fins. Additionally, the amount of red also appears to increase with the age of the fish. Some female *N. kadleci* have irregular black dots on their bodies (especially at MZCS-08/107, but also MZCS-08/91) which is characteristic for some populations of *N. orthonotus* (especially in vicinity of the city of Beira), but lacking in all known *N. furzeri* populations.

The Save River forms an apparent range boundary between *N. kadleci* (north of the Save) and *N. furzeri* (south of the Save). This is confirmed by a thorough sampling effort (Wood 2000; Terzibasi *et al.* 2008; Reichard *et al.* 2009). The species status is supported by the analysis of mitochondrial and nuclear DNA markers (Reichard *et al.*, unpublished data), with *N. kadleci* being a sister species of *N. furzeri*.

Two populations of *Nothobranchius kadleci* were imported and are bred in the aquarium facilities of the Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, and distributed among dedicated killifish breeders under the names *Nothobranchius* sp. *aff. furzeri* MZCS-08/91 Gorongose and *Nothobranchius* sp. *aff. furzeri* MZCS-08/108 Save. It should be noted that the fish described here as *N. kadleci* was collected in central Mozambique in May 1970 on the floodplain of the Pungwe River by D.

Plowes (R. Wildekamp, personal communication) and in 1973 in the vicinity of the town Vila Machado (now Nhamatanda) in the Pungwe River basin by D. G. Donnelly (B. Watters, personal communication). It has never been recollected and it was regarded as a very red colour form of *N. orthonotus* (known as *Nothobranchius* sp. Vila Machado) (B. Watters, personal communication). All subsequent collections in the area were performed in April or May after the cessation of the rainy season. In contrast, our sampling was carried out in February (during the rainy season). It is possible that, similar to *N. furzeri*, *N. kadleci* is a short-lived species inhabiting shallow pools that desiccate earlier than those inhabited by other *Nothobranchius* species in the area. Indeed, within the same site *N. kadleci* were often found in shallower pools, while adjacent (<10 m) deeper pools were inhabited by *N. orthonotus* and *N. rachovii*. At other sites, all three species were syntopic at the time of collection. *Nothobranchius kadleci* has never been recorded in lowland floodplains (such as in the vicinity of Beira).

In conclusion, *N. kadleci* may be a short-lived rather than rare species and occurs in a range of small temporary pools between the Save and Zambezi River. It is expected that it might play an important role in the comparative research on aging where *N. furzeri* (from drier regions than *N. kadleci*) is becoming a model species due to its short lifespan (Valdesalici & Cellerino 2003; Genade *et al.* 2005; Terzibasi *et al.* 2007; Terzibasi *et al.* 2008)

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