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Xenopus laevis as UberXL for nematodes

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The effect of invasive species on local parasite dynamics is often overlooked. The African Clawed Frog *Xenopus laevis* (Daudin, 1802) (Anura: Pipidae) is a global invader, with established populations on four continents and is a domestic exotic in southern Africa. Despite a century of parasitological surveys, the current study reports seven previously unrecorded nematode species parasitising *X. laevis* across South Africa. These are adult *Capillaria* sp. and *Falcaustra* sp. from the intestine, third stage larvae of *Contraecum* sp. encysted in the body cavity, third stage larvae of *Paraquimperia* sp. and *Tanqua* sp. from the intestine and two different species of second stage nematode larvae from the lungs and kidneys, respectively. Morphological descriptions, photomicrographs and molecular data of the 18S and 28S rRNA and COI genes are provided to aid future investigations. We propose that these nematodes could well be using *X. laevis* as a definitive, paratenic and intermediate host, probably involving native fish, piscivorous birds, semi-aquatic reptiles and invertebrates in their life cycles. All recovered nematodes are recorded for the first time herein in association with *X. laevis*, except for the genus *Contraecum*, members of which have previously been recorded from invasive *X. laevis* from California and Chile. The current study illustrates that *X. laevis* is an important parasite reservoir in its native range, with implications for its role in the invasive range. The fact that none of these nematodes could be identified to species level underscores the importance of providing morphological descriptions and molecular data when reporting on parasitological surveys, especially those of known invasive species.

Keywords: African clawed frog, *Capillaria*, *Contraecum*, *Falcaustra*, *Paraquimperia*; parasite reservoir, *Tanqua*

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Introduction

Biological invasion, or the translocation of animals, plants and pathogens to novel habitats, often with human help, is one of the distinguishing characteristics of the Anthropocene (Ellis et al. 2012; Capinha et al. 2015). In numerous cases, declines in biodiversity are directly linked to the spread of highly competitive, generalist invasive species (Ricciardi 2007; Bellard et al. 2016) and many invasive species impact their new ecosystems negatively (Simberloff 2011).

In particular, the role of invasive species in the alteration of parasite dynamics in their novel habitats is frequently overlooked (Blackburn and Ewen 2017). Conversely, introduced hosts could cause the amplification of native parasite dynamics, by acting as reservoirs for native parasites that can eventually spill back to native hosts, or conversely, they can dilute these interactions by acting as dead-end hosts for native parasites (Telfer and Bown 2012). These ripples can be felt several links down the food chain, especially in the case of parasites transmitted via trophic interactions (Amundsen et al. 2013).

The globally invasive African clawed frog, *Xenopus laevis* (Daudin, 1802) (Anura: Pipidae) is one of the world's most

widely distributed amphibian invaders. Its human-mediated range expansion was initiated in the 1930s through its use as a biological pregnancy assay and a model research animal and later with the help of the pet trade (Gurdon and Hopwood 2000; Weldon et al. 2007; van Sittert and Measey 2016). Currently, its invasive range spans four continents, with established populations mainly in areas with a Mediterranean climate (Lobos and Measey 2002; Measey et al. 2012). However, climate and niche modelling have made it clear that *X. laevis* still has many potential environments to fill across the globe (Measey et al. 2012; Ihlw et al. 2016; van Sittert and Measey 2016; Rödder et al. 2017).

In addition to its status as global invader, *X. laevis* exhibits recurring range expansion within its native range (Measey and Davies 2011; Measey et al. 2017). These domestic invasions were brought about by its frequent translocation for research and training purposes in the past (van Sittert and Measey 2016) and continues to the here and now through natural dispersal via overland movement and artificial waterbodies (Measey 2004; Measey et al. 2012; Measey 2016; de Villiers and Measey 2017).

The parasite fauna of *X. laevis* has received extensive attention since the early 1900s, with more than 25 parasitic genera, representing all invertebrate parasite groups, except acanthocephalans, described in association with this host in its native range (Tinsley 1996). Although the parasite communities of invasive *X. laevis* are significantly impoverished (Schoeman et al. 2019), at least three of its coevolved parasites have been cointroduced across the invasive range (Tinsley and Jackson 1998b; Jackson and Tinsley 2001a; Kuperman et al. 2004; Rodrigues 2014; Schoeman et al. 2019). These are the monogeneans *Protopolystoma xenopodis* Price, 1943 and *Gyrdicotylus gallieni* Vercammen-Grandjean, 1960 and the cestode *Cephalochlamys namaquensis* Cohn, 1906 (see Schoeman et al. 2019).

Notably, host-specific parasites with complex life cycles are absent from the accompanying parasite assembly (Schoeman et al. 2019). Notwithstanding, it is specifically the digeneans and nematodes native to the invasive range of *X. laevis* that have been able to form novel host-parasite associations with the new invader (Kuperman et al. 2004; Rodrigues 2014; Castillo et al. 2017; Schoeman et al. 2019).

In the case of nematodes, Kuperman et al. (2004) reported juvenile stages of *Contracaecum* Rialet et Henry, 1912 (Ascaridoidea: Anasakidae) from the body cavity and *Eustrongylides* Jägerskiöld, 1909 (Dioctophymatoidea: Dioctophymidae) from the subcutaneous tissue in the Californian invasive population of *X. laevis*. In addition, *Contracaecum* larvae were also recorded at very low infection levels encapsulated in the intestinal serosa of *X. laevis* invasive in Chile (Castillo et al. 2017). Both sets of authors proposed the native parasite fauna of California and Chile to be the source of the infections, because none of these parasites have been reported in association with *X. laevis* from southern Africa (Kuperman et al. 2004; Castillo et al. 2017).

In turn, in the native range, the Nematoda is the second most speciose taxon among the parasites of *X. laevis* after the Digenea (Tinsley 1996). Of these, three species belong to the Family Camallanidae (Camallanoidea), namely *Batrachocamallanus slomei* (Southwell et Kirshner, 1937), *Camallanus kaapstaadi* Southwell et Kirshner, 1937 and *C. xenopodis* Jackson et Tinsley, 1995. These species are found across Africa in *Xenopus* spp. (Southwell and Kirshner 1937; Kung 1948; Yeh 1960b; Thurston 1970; Avery 1971; Tinsley et al. 1979; Jackson and Tinsley 1995a, 1995b; Svitin et al. 2018) and *C. kaapstaadi* has been found to infect crocodylians through post-cyclic parasitism (Junker et al. 2019). Another described nematode is *Pseudocapillarioides xenopi* Moravec et Cosgrove, 1982 (Enoplida: Capillariidae), of which all the life stages infest the skin of *X. laevis* (see Cosgrove and Jared 1974; Cosgrove and Jared 1977; Moravec and Cosgrove 1982; Wade 1982; Cohen et al. 1984; Stephens et al. 1987; Brayton 1992; Feldman and Ramirez 2014).

A few reports of unidentified nematodes described in association with *X. laevis* across its native range have arisen over the years, ranging from a single specimen of probably *Rhabdias* Stiles et Hasal, 1905 (Rhabditoidea: Rhabdiasidae) in the lung (Cosgrove and Jared 1974)

and two species of quimperiid nematodes (Ascaridoidea: Quimperiidae) in the intestine (Thurston 1970), to unidentified nematodes encysted in body tissues (Cosgrove and Jared 1974). Larval nematodes in the glomerular space were also reported (Cosgrove and Jared 1974; Brayton 1992). These reports, though rare, suggest that *X. laevis* could act as a paratenic or intermediate host for some nematodes in its native range, as it has already proven itself to be capable of this in the invasive range.

In light of the pervasive effects of tropically transmitted parasites in biological invasions (Dunn et al. 2012; Roy and Lawson Handley 2012; Amundsen et al. 2013), it is paramount to have a better understanding of the role of *X. laevis* in the parasite dynamics of its native ecosystems. To this end, as part of a larger parasitological survey of *X. laevis* across the whole of its native range, the current study is the first report of seven nematode species parasitising this host in South Africa. Short morphological descriptions, supported by photomicrographs and molecular data (18S and 28S rRNA and the COI gene sequences), as well as distribution information, are provided for future reference in the native range and beyond. Furthermore, possible avenues of parasite transmission are explored, based upon a survey of the literature.

Materials and methods

In total, 181 adult individuals were collected in chicken liver baited funnel traps from 28 localities across South Africa from March 2017 to April 2019 (see Supplementary Table S1 for detailed information on all collection sites). The frogs were anaesthetised in 6% ethyl-3-aminobenzoate methanesulfonate (MS222) (Sigma-Aldrich Co., St. Louis, Missouri, United States) and subsequently euthanised through pithing, according to internationally accepted standard operating procedures. For the external parasite examination, the epidermis, lateral line, eyes, buccal cavity, eustachian tubules and nostrils were examined. Thereafter, the body was slit open longitudinally and the alimentary tract, kidney, excretory bladder, gallbladder with bile ducts, liver, lungs, heart and reproductive organs were removed and examined separately using a stereomicroscope in 0.6% amphibian saline, prepared according to Ringer's method (du Preez and van Wyk 2007), for internal parasites. The acquired nematodes were washed in saline, fixed in 70% hot ethanol and subsequently stored in 70% ethanol.

Prior to microscopic examination, the nematodes were placed in distilled water for about 20 min and then cleared in lactophenol for a period of time ranging from 30 min to 24 h, depending on the size of the respective nematode. The morphology of the nematodes was studied and photomicrographs taken using ZEISS Axio Z1, Nikon AZ100, Nikon E800 and Nikon ECLIPSE Ni compound microscopes. Measurements were taken with the aid of the software ZEN (blue edition) (Carl Zeiss Microscopy GmbH, Jena, Germany) and NIS-Elements Documentation version 3.22.09 (Nikon Instruments Inc., Tokyo, Japan). In total, two of nine *Capillaria* sp. Zeder, 1800 females, nine of 183 *Contracaecum* sp. larvae, seven *Falcaustra* sp. Lane, 1915 (three females and four males), two of four *Paraquimperia* sp. Baylis, 1934 larvae, four of nine

Tanqua sp. Blanchard, 1904 larvae, 14 of approximately 1 035 unidentified nematode larvae sp. 1, and eight of approximately 150 unidentified nematode larvae sp. 2 were measured. All measurements in the text are given in micrometres, unless stated otherwise, and presented as mean values, followed by ranges in parentheses. For molecular studies, the middle fragments of specimens were used, whereas the taxonomically important anterior and posterior parts were reserved for the morphological identification of species.

DNA was extracted using the PCR BIO Rapid Extract PCR Kit (PCR Biosystems Ltd., London, United Kingdom). Cytochrome oxidase c subunit I (COI) amplicons were obtained using the primer pair 'LC01490' (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and 'HCO2198' (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al. 1994). The thermocycling profile was as follows: 3 min denaturation at 94 °C, 20 cycles of 94 °C for 30 s, 45 °C for 30 s, 72 °C for 1 min and 40 cycles of 94 °C for 30 s, 51 °C for 1 min, 72 °C for 1 min for amplification and finally 72 °C for 10 min for extension. The 18S rRNA was amplified by the primer pair 'F18ScF1' (5'-ACC GCC CTA GTT CTG ACC GTA AA-3') and 'F18ScR1' (5'-GGT TCA AGC CAC TGC GAT TAA AGC-3'), with the following thermocycling profile: 5 min denaturation at 95 °C, 40 cycles of 95 °C for 30 s, 58 °C for 30 s, 72 °C for 1 min 30 s for amplification, followed by an extension of 7 min at 72 °C (Lefoulon et al. 2015). The 28S rRNA was amplified using the primer pair 'LSU5' (5'-TAG GTC GAC CCG CTG AAY TTA AGC A-3') and 'LSU3' (5'-TAG AAG CTT CCT GAG GGA AAC TTC GG-3') (Littlewood et al. 1997), with the thermocycling profile as follows: one initial step of 5 min at 95 °C for long denaturation; 35 cycles of 1 min at 95 °C for denaturation, 2 min at 48 °C for annealing and 2 min at 72 °C for elongation and one final step of 10 min at 72 °C for terminal elongation (Verneau et al. 2009). For purification and sequencing, PCR products were sent to a commercial company (Inqaba Biotec, Pretoria, South Africa) that used the ExoSAP protocol (New England Biolabs Ltd., Massachusetts, United States) for purification. Sequencing was performed via BigDye® Terminator version 3.1 Cycle Sequencing, utilising the corresponding primer pairs used for the final PCR reaction, on an ABI3500XL analyser (Applied Biosystems™). Contiguous sequences were assembled and edited using Geneious version 9.0 (Saint Joseph, Missouri, United States) and submitted to GenBank.

For each nematode species, prevalence, mean infection intensity and mean abundance were calculated for the localities where the species was present, *sensu* Bush et al. (1997).

All applicable institutional, national and international guidelines for the care and use of animals were followed under the North-West University ethics approval number NWU-00380-16-A5-01.

Results

During the course of the current study, seven species of nematodes were discovered in association with *X. laevis* at ten localities across South Africa (Figure 1). Some species, such as the *Contracaecum* sp. encysted third stage larvae,

were quite common across the region, whereas other infections were more localised. The unidentified second stage larvae from the lungs had the highest abundance and infection intensity of all at the three localities where it occurred (Table 1).

Nematode descriptions

Capillaria sp.

Site of infection: Stomach, intestine and rectum

Representative DNA sequences: 28S rRNA (MN526255)

Description

Females (Figure 2). Measurements based on two gravid specimens. Body elongated, thin at anterior part widening posteriorly, 9.4–15.6 mm long, 58–66 µm wide. Anterior and posterior ends rounded. Muscular oesophagus elongated, evenly widening towards posterior end, 272–324 µm long. Stichosome almost cylindrical along whole length, 2.3–2.7 mm long. Stychocytes wider than long, with often indistinct merges. Total oesophagus 2.7–3.0 mm long. Nerve ring encircling oesophagus at level of its anterior half, 107–121 µm from anterior end of body. Vulva pre-equatorial, with thick walls, situated at 2.9–4.6 mm from anterior end of body, comprising 29–31% of body length. Vulva with 76–238 eggs, arranged in one row near vulva and in three rows posteriorly. Eggs 41–54 µm (mean 50 µm) long, 20–26 µm (mean 23 µm) wide ($n = 10$). Intestine straight, narrow, rectum short, with thick walls. Tail short, rounded, subterminal.

Remarks

Of the capillariid nematodes, only *Pseudocapillaroides xenopi* has been described in association with *X. laevis* imported to Europe from South Africa (Moravec and Cosgrove 1982; Wade 1982). This species was described by Moravec et Cosgrove 1982 as *Pseudocapillaroides xenopi*. In the same year, Wade described it as *Capillaria xenopodis*. These two names were used interchangeably. However, *P. xenopi* is regarded as the generally accepted one (see Feldman and Ramirez 2014), because the species clearly belongs to a genus separate from *Capillaria*, based upon both phylogenetic and morphological evidence. Representatives of *Pseudocapillaroides* Moravec et Cosgrove, 1982 are characterised by the eggs containing developed larvae, small body size and the subcutaneous site of infection (Moravec and Cosgrove 1982; Wade 1982).

Other reports of capillariids from Africa have been registered throughout southern Africa from different species of clariid and cyprinid fish. However, in most cases, these nematodes were recorded without descriptions and identified only to genus level (Boomker 1994a; Moyo et al. 2009). In our material, only female specimens (of which two harboured well-developed eggs) were found in the host intestines. Based on the general body measurements, the morula stage of the eggs and the site of infection, as well as the molecular data, we assign our specimens to the genus *Capillaria*. Unfortunately, because of an absence of males and a lack of clear molecular data, we could not identify them to the species level.

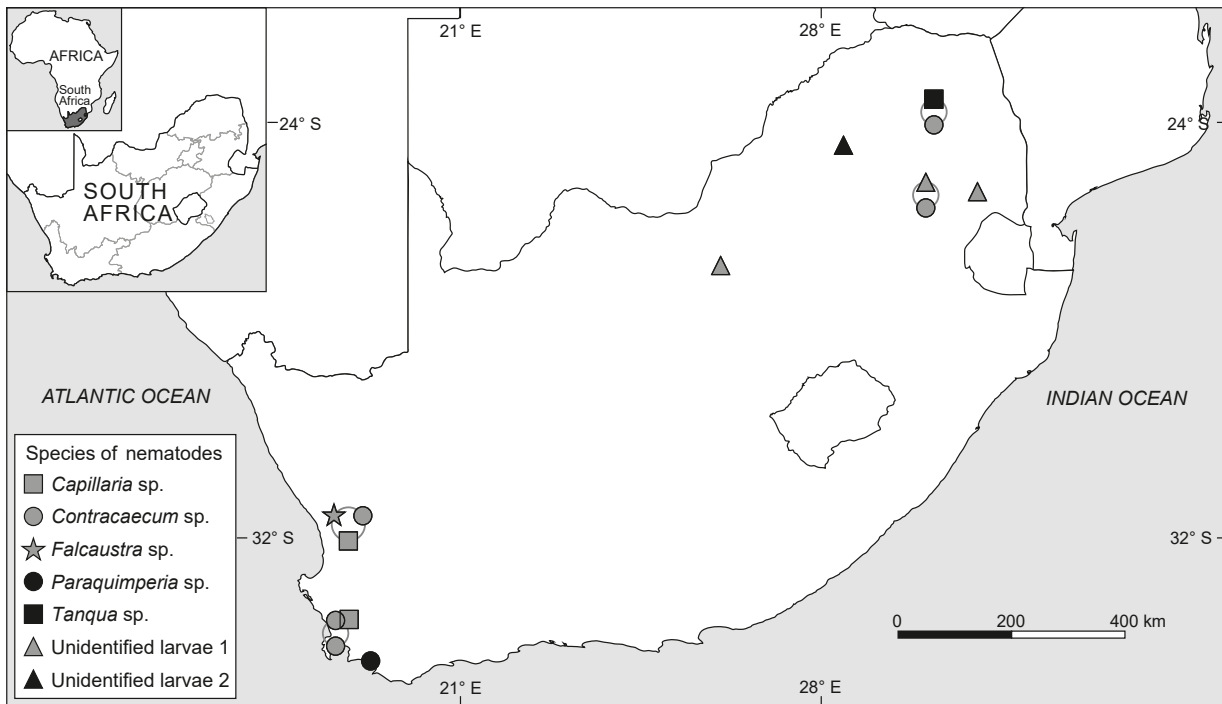


Figure 1: Distribution of seven previously undescribed species of nematodes recovered at ten localities across South Africa during the parasitological screening of *Xenopus laevis*. The presence of more than one nematode species in hosts from a single locality (Dullstroom, Vanrhynsdorp and Tzaneen), or from two localities in close proximity (in Cape Town), is denoted by the arrangement of the symbols in a ring around the central point. All maps utilise the Mercator projection and were created in QGIS 3.4.3 *Madeira*

***Contraeaecum* sp.**

Site of infection: Encysted in the body cavity and on the outer surfaces of stomach and liver.

Representative DNA sequences: COI (MN526248), 18S rRNA (MN526250), 28S rRNA (MN526256)

Description

Third stage larva (Figure 3). Measurements based on nine specimens. Body comparatively thick, robust, 42.0 mm (28.0–49.0 mm) long, 810 μ m (550–925 μ m) wide. Along entire body cuticle, with conspicuous transverse striations. Anterior end rounded, bearing small ventral cuticular tooth. Excretory pore situated near tooth. Oesophagus elongated, almost cylindrical in anterior half, widening posteriorly. Oesophagus 3.1 mm (2.8–3.5 mm) long, 8.0% (6.6–11.0%) of body length; 92 μ m (77–116 μ m), 143 μ m (106–192 μ m) and 180 μ m (99–230 μ m) wide at anterior, midlength and posterior part, respectively. Nerve ring encircling oesophagus at level of its anterior end, at 492 μ m (363–547 μ m) from anterior end of body; 16% (12–18%) of oesophagus length. Intestine straight, narrow. Rectum short, with thick walls. Tail tapering, 186 μ m (135–247 μ m) long.

Remarks

Third stage larvae of *Contraeaecum* have been found encapsulated in the body cavity of numerous fish species throughout southern Africa: spot-tail robber *Brycinus imberi*, African sharp-tooth catfish *Clarias gariepinus* and African blunt-tooth catfish *C. ngamensis*, canary kurper

Chetia flaviventris, redbreast tilapia *Coptodon rendalli*, common carp *Cyprinus carpio*, papermouth *Enteromius mattozi*, threespot barb *E. trimaculatus*, African pike *Hepsetus odoe*, tigerfish *Hydrocynus vittatus*, largescale yellowfish *Labeobarbus marequensis*, bulldog *Marcusenius macrolepidotus*, largemouth bass *Micropterus salmoides*, Mozambique tilapia *Oreochromis mossambicus*, threespot tilapia *O. andersonii*, greenhead tilapia *O. macrochir*, Cape kurper *Sandelia capensis*, dusky bream *Sargochromis codringtonii*, butter catfish *Schilbe intermedius*, Zambezi bream *Serranochromis robustus*, purpleface largemouth *S. macrocephalus*, blackspotted squeaker *Synodontis nigromaculatus* and banded tilapia *Tilapia sparrmanii* (see Whitfield and Heeg 1977; Mashego and Saayman 1981; Boomker 1982; van As and Basson 1984; Mashego 1989; Boomker 1994a, 1994b; Barson 2004; Barson and Avenant-Oldewage 2006; Barson et al. 2008; Boane et al. 2008; Moyo et al. 2009; Madanire-Moyo et al. 2010; Smit and Luus-Powell 2012; Sara et al. 2014; Mbokane et al. 2015; Moravec and van As 2015; Tavakol et al. 2015; McHugh et al. 2016; Moravec et al. 2016). Nevertheless, only Moravec et al. (2016) provided detailed descriptions (including line drawings and SEM images) of *Contraeaecum* sp. from the Cape kurper *S. capensis* from South Africa. Of the *Contraeaecum* species known from South Africa, only the gene fragments of *C. ogmorhini* Johnston et Mawson, 1941 from the Cape fur seal *Arctocephalus pusillus* are available in GenBank (Nadler et al. 2000; Zhu et al. 2001; Shamsi et al. 2009; Jabbar et al. 2013). Because the morphology of the third stage larvae of

Table 1: Complete locality data and infection parameters, *sensu* Bush et al. (1997), of the seven nematode species reported for the first time from the African clawed frog *Xenopus laevis* from ten localities in South Africa. Locality names are given as farm name, nearest town and province. Values are reported as the mean for a given locality and species, with the median in square brackets and the range in round brackets

Nematode	Locality	Coordinates	Number of hosts collected	Intensity	Abundance	Prevalence
<i>Capillaria</i> sp.	7-Fontein Farm, Vanrhynsdorp, Western Cape	31°44'09.8" S, 18°49'31.7" E	7	2 [2] (1–2)	0.4	29%
	Loekiesfontein Farm, Wellington, Western Cape	33°34'16.9" S, 18°50'24.4" E	6	2 [1] (1–4)	0.8	38%
<i>Contraecum</i> sp.	7-Fontein Farm, Vanrhynsdorp, Western Cape	31°44'09.8" S, 18°49'31.7" E	7	2 [2] (1–2)	0.4	29%
	Bloemendal Wine Estate, Cape Town, Western Cape	33°50'21.2" S, 18°36'01.0" E	5	3	0.6	20%
	Burgundy Estate, Cape Town, Western Cape	33°50'07.8" S, 18°33'10.1" E	14	5 [5] (4–6)	0.7	14%
	Crimson Creek Cherry Farm, Dullstroom, Mpumalanga	25°23'53.2" S, 30°02'16.9" E	10	3 [2] (1–8)	1.7	50%
	Letsitele, Tzaneen, Limpopo	23°47'55.7" S, 30°11'42.5" E	10	1	0.1	10%
<i>Falcaustra</i> sp.	7-Fontein Farm, Vanrhynsdorp, Western Cape	31°44'09.8" S, 18°49'31.7" E	7	2 [2] (1–3)	1.1	57%
<i>Paraquimperia</i> sp.	Hermanus, Western Cape	34°22'12.6" S, 19°15'25.4" E	10	4	0.4	10%
<i>Tanqua</i> sp.	Letsitele, Tzaneen, Limpopo	23°47'55.7" S, 30°11'42.5" E	10	5 [5] (1–8)	0.9	20%
Unidentified nematode larvae sp. 1	Crimson Creek Cherry Farm, Dullstroom, Mpumalanga	25°23'53.2" S, 30°02'16.9" E	10	76 [76] (1–150)	15.1	20%
	Jacana Estate, White River, Mpumalanga	25°20'20.7" S, 31°01'21.2" E	8	11 [11] (5–16)	2.6	25%
	Potchefstroom, North-West Province	26°45'19.7" S, 26°03'02.2" E	9	145 [30] (5–720)	112.7	78%
Unidentified nematode larvae sp. 2	Placidus Farm, Modimolle, Limpopo	24°26'18.1" S, 28°26'12.8" E	6	150	25.0	17%

different *Contraecum* species is almost indistinguishable and our specimens clearly differed from *C. ogmorhini* (KU558726) in the COI alignments (only 582 of 689 bp are identical for both species), we could only identify the recovered specimens to genus level.

***Falcaustra* sp.**

Site of infection: Intestine and stomach

Sequences for this species could not be obtained.

Description

General (Figure 4). Comparatively short nematodes, with maximum width at body midlength. Apical: three large anterior labia, with two circles of papillae (six inner and six outer), oral opening rounded-triangular shape. Oesophagus long, consisting of short anterior pharyngeal region, long cylindrical corpus, short, slightly expanded isthmus and well-developed posterior bulb. Nerve ring encircling oesophagus at level of its anterior quarter. Excretory pore at level of oesophageal bulb. Tail tapering, with sharpened end in both sexes.

Males. Measurements based on four specimens. Body 7.3 mm (mean 5.4–9.3 mm) long, 197 µm (mean 143–281 µm) wide. Oesophagus 1.3 mm (1.1–1.5 mm) long, 19% (16–21%) of body length; 37 µm (31–47 mm),

62 µm (44–77 µm) and 136 µm (110–159 µm) wide at anterior, midlength and posterior level, respectively. Nerve ring at 321 µm (294–345 µm) from anterior end, 24% (22–29%) of oesophagus length. Excretory pore at 1 038 µm (741–1 193 µm) from anterior end. Posterior end of body coiled ventrally. Spicules equal, sharpened at tips, 380 µm (318–453 µm) long. Gubernaculum short, narrowing towards posterior end, 84 µm (65–102 µm) long. Caudal end with papillae: three pairs preloacal, one unpaired papilla just anterior to cloaca, six pairs post cloacal (three pairs of subventral papillae and one pair of lateral papillae anterior to cloaca plus two subventral pairs close to tail tip). Phasmids at level of tail midlength. Tail tapering, 285 µm (240–321 µm) long.

Females. Measurements based on three specimens. Body 8.3 mm (6.7–9.7 mm) long, 191 µm (163–222 µm) wide. Oesophagus 1.6 mm (1.5–1.9 mm) long, 20% (19–22%) of body length; 48 µm (41–57 µm), 68 µm (65–72 µm) and 152 µm (142–165 µm) wide at anterior, midlength and posterior level, respectively. Nerve ring at 380 µm (370–390 µm) from anterior end, 23% (21–25%) of oesophagus length. Excretory pore at 1 277 µm (1 110–1 396 µm) from anterior end. Vulva postequatorial, 5.5 mm (4.3–6.6 mm) from anterior end, 66% (64–68%) of body length. Tail tapering, 403 µm (355–489 µm) long.

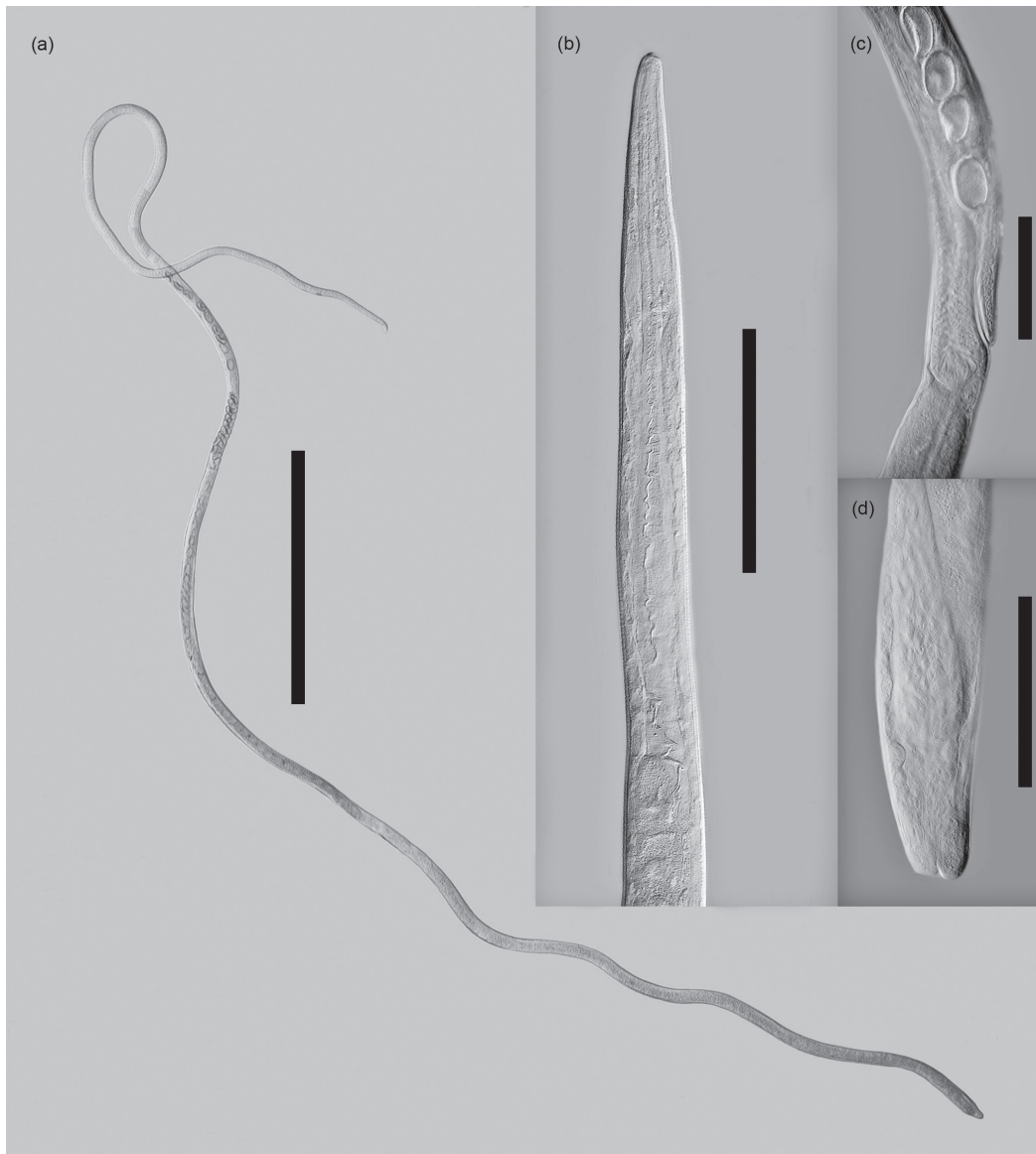


Figure 2: Adult female of *Capillaria* sp. from the digestive tract of *Xenopus laevis*, photomicrographs. (a) general view; (b) anterior end of body, lateral view; (c) part of body at vulva region, lateral view; (d) posterior end of body, lateral view. Scale bars: (a): 1 mm; (b-d): 100 µm

Remarks

The examined specimens were assigned to the genus *Falcaustra*, because of the presence of three well-developed labia and a differentiated oesophageal bulb, with well-developed valves (Anderson 2000). Our specimens differed from most of the other African species of *Falcaustra* described from fish and terrapins by the absence of a pseudosucker on the male tail (Baker 1983; Moravec and Scholtz 2017). The same parameter is described for the three fish-parasitising species, namely *F. piscicola* (von Linstow, 1907), *F. verbekei* Campana-Rouget, 1961 and *F. therezieni* Petter, 1979 and for the two species from amphibians, namely *F. hinkeli* Jackson, 2000 and *F. puylaerti* Jackson, 2000 from *Xenopus* spp. (including *X. laevis*) (Jackson 2000). The specimens from our material differ from the

latter two species in metrical characters, such as size of the gubernaculum (65–102 µm in *Falcaustra* sp. vs 44–65 µm and 42 µm in *F. hinkeli* and *F. puylaerti*, respectively), length of the spicules (318–453 µm in *Falcaustra* sp. vs 151 µm in *F. puylaerti*) and length of the female tail (350–489 µm in *Falcaustra* sp. vs 560–1 060 µm in *F. hinkeli*) in comparably sized worms. *Falcaustra* sp. also clearly differs from the fish-parasitising species by the number of post-cloacal papillae: it has six pairs, whereas *F. piscicola* possesses eight pairs and *F. verbekei* and *F. therezieni* possess seven pairs (Yorke and Maplestone 1926; Bursey and Rivera 2009). Despite the clear morphological differences, we prefer not to describe a new species, but rather to assign the recovered specimens to *Falcaustra* sp., as a result of the limited sample size and lack of gravid females.

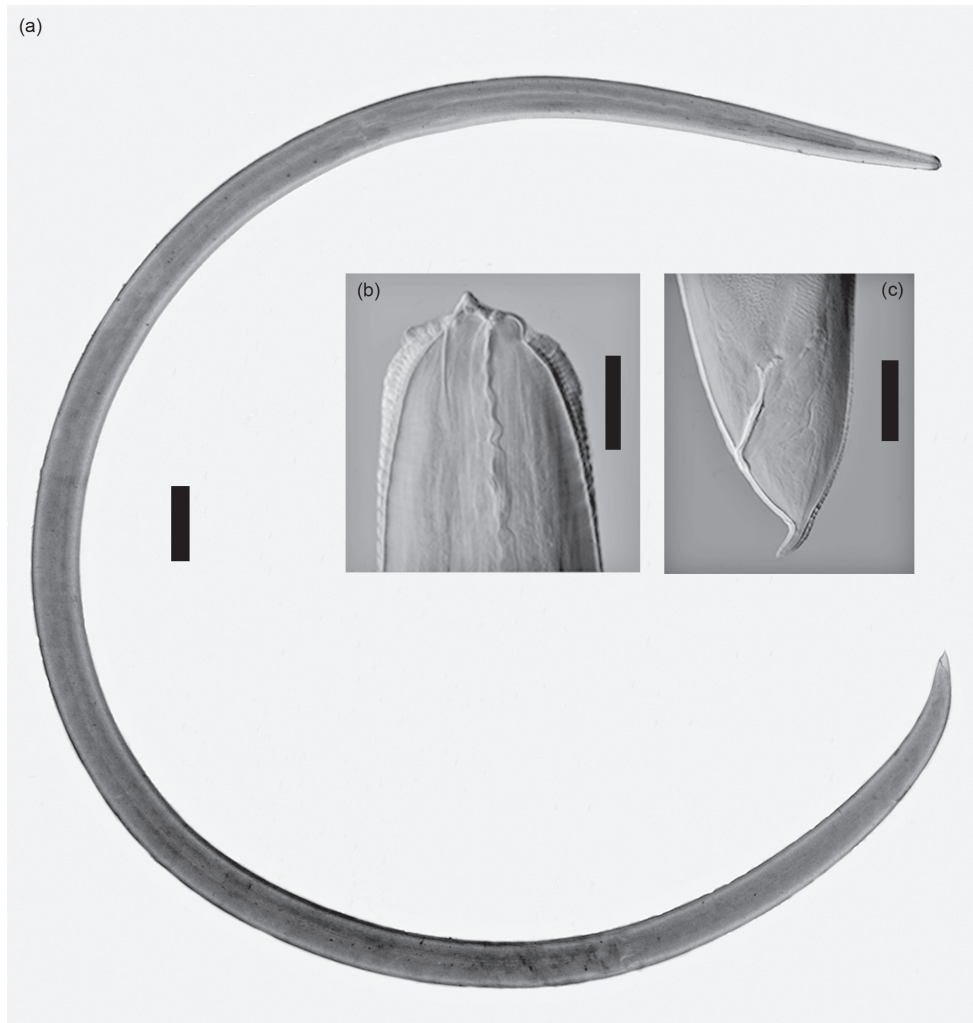


Figure 3: Third stage larval *Contracaecum* sp. encysted in *Xenopus laevis*, photomicrographs. (a) general view; (b) anterior end of body, lateral view; (c) posterior end of body, lateral view. Scale bars: (a): 1 mm; (b), (c): 100 µm

***Paraquimperia* sp.**

Site of infection: Intestine

Representative DNA sequences: COI (MN526249), 18S rRNA (MN526251), 28S rRNA (MN526257)

Description

Third stage larva (Figure 5). Measurements based on two specimens. Body thin, elongated, 4.0–5.7 mm long, 77–114 µm wide. Oesophagus club-shaped, 416–712 µm long, 7–18% of body length; 12–13, 21–25, 20–27 and 52–69 µm wide at anterior, anterior dilation, midlength and posterior bulb level, respectively. Nerve ring encircling oesophagus at anterior half, at 170–211 µm from anterior end of body; 30–41% of oesophagus length. Excretory pore (found in one specimen) at 436 µm from anterior end of body. Genital primordium small, situated at midbody region. Tail short, tapering 218–290 µm long.

Remarks

The recovered specimens corresponded to *Paraquimperia africana* (JF803925) in 99% of their 18S rRNA fragments

(683 of 684 bp are identical for both species) (Moravec 2007). The genus *Paraquimperia* currently includes only three species, found in the intestines of eels and additionally reported from several cyprinid and percid fish (Šrámek 1901; Baylis 1934; Mueller 1934; Karve 1941; Yamaguti 1961; Moravec 1966a, 1966b; Hanek and Threlfall 1970; Hanek and Molnar 1974; Ivashkin and Khromova 1976; Jackson 1978; Naidu 1983; Gupta and Bakshi 1984; Køie 1988; Saraiva and Chubb 1989; Nie and Kennedy 1991; Cone et al. 1993; Moravec 1994; Marcogliese and Cone 1996; Moravec et al. 2000; Thielin et al. 2007; Sasal et al. 2008; Lin et al. 2015). The only species described from Africa is *P. africana* Moravec, Boomker et Taraschewski, 2000 (Jackson 1978; Moravec et al. 2000). Because 18S rRNA is very conservative, a difference of one nucleotide in a comparatively short fragment could be considered as interspecific. Therefore, until numerous sequences of different genes from different species have been obtained, we prefer to assign the recovered specimens to *Paraquimperia* sp.

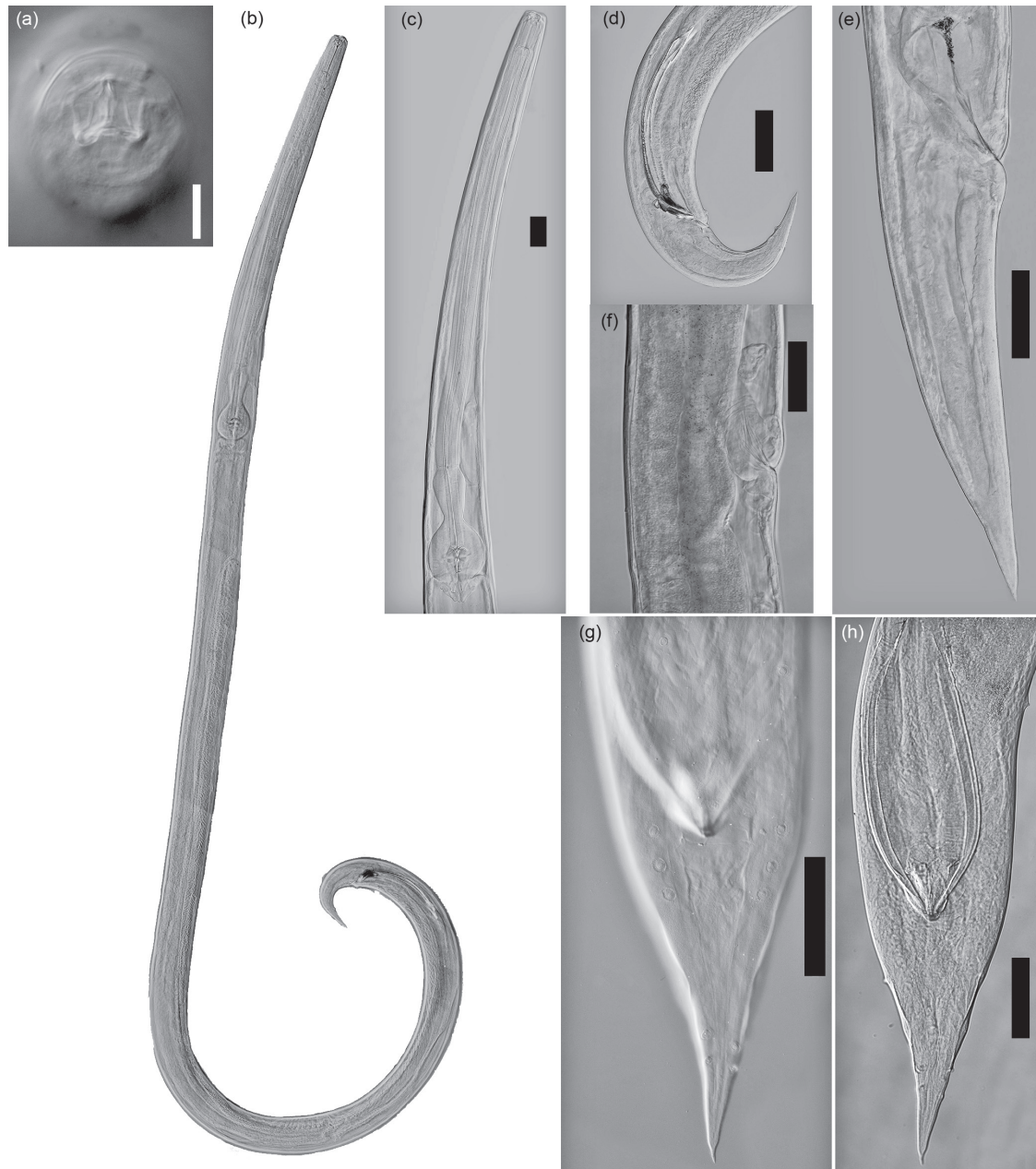


Figure 4: Adult *Falcaustra* sp. from the digestive tract of *Xenopus laevis*, photomicrographs. (a) anterior end of body, male, apical view; (b) male, general view; (c) anterior end of body, male, lateral view; (d) posterior end of body, male, lateral view; (e) posterior end of body, female, lateral view; (f) part of body at vulva region, lateral view; (g), (h) posterior end of body, male, ventral view. Scale bars: (a): 50 μ m; (b): 1 mm; (c-h): 100 μ m

***Tanqua* sp.**

Site: Encysted in the intestine

Representative DNA sequences: 18S rRNA (MN526252), 28S rRNA (MN526258)

Description

Third stage larva (Figure 6). Measurements based on four specimens. Body thin, elongated, with maximum width at midlength level. Body 10.0 mm (8.8–10.8 mm) long, 292 μ m (281–315 μ m) wide. Anterior end with two minute pseudolabia, not reaching each other. Oesophagus

elongated, evenly widening towards posterior end, 2.8 mm (2.6–3.0 mm) long, 28% (27–30%) of body length; 41 μ m (37–47 μ m), 117 μ m (79–137 μ m), 174 μ m (153–203 μ m) wide at anterior, midlength and posterior level, respectively. Nerve ring encircling oesophagus at its anterior end, 316 μ m (294–338 μ m) from anterior end, 11% (11–11%) of oesophagus length. Excretory pore situated at 411 μ m (372–443 μ m) from anterior end, 4% (4–4%) of body length. Tail short, tapering, with rounded tip, 180 μ m (162–197 μ m) long.

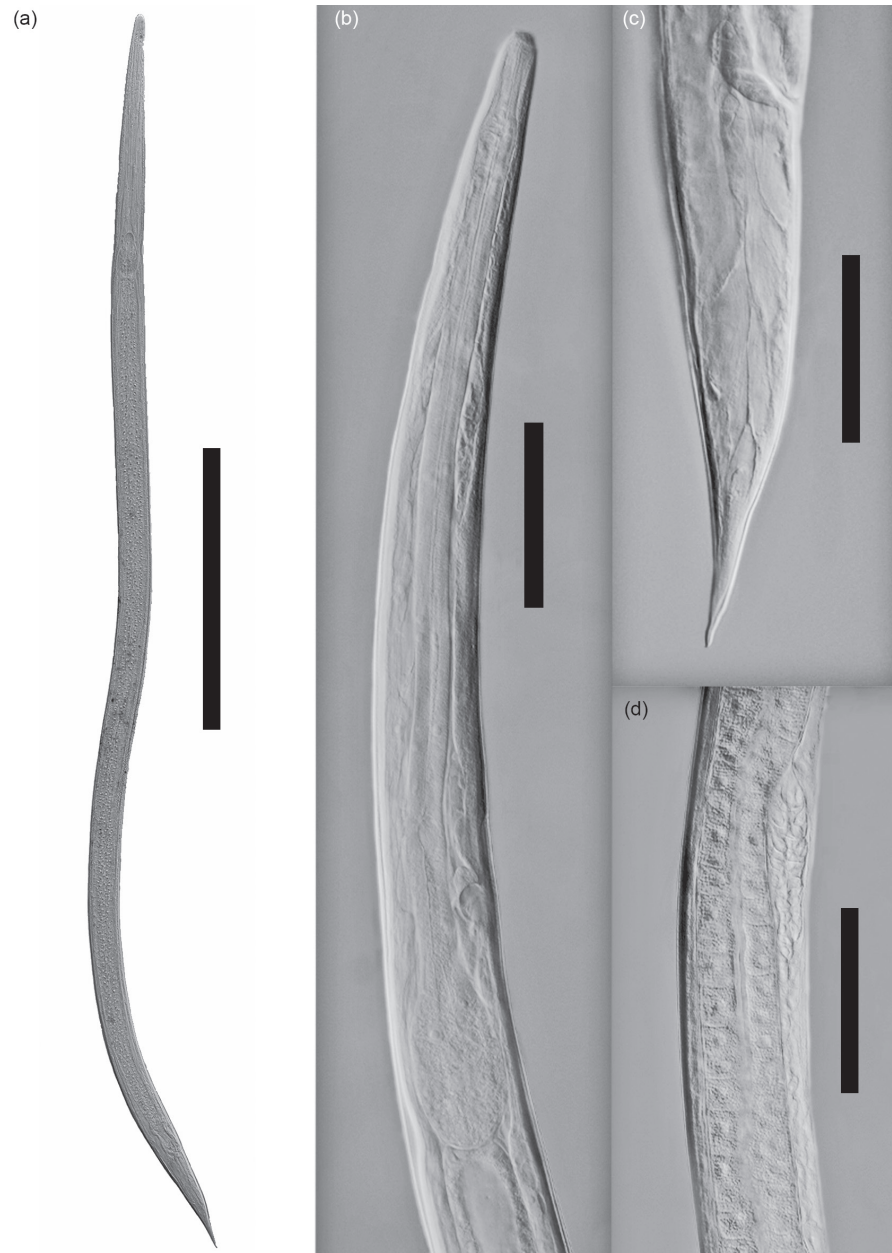


Figure 5: Third stage larval *Paraquimperia* sp. from the digestive tract of *Xenopus laevis*, photomicrographs. (a) general view; (b) anterior end of body, lateral view; (c) posterior end of body, lateral view; d) fragment of body at genital primordium region, lateral view. Scale bars: (a): 1 mm; (b-d): 100 μ m

Remarks

Representatives of the genus *Tanqua* are specific parasites of various species of *Varanus* lizards. Only *Tanqua tiara* (von Linstow, 1879) has previously been reported from South Africa from *V. albigularis* and *V. ornatus* (von Linstow 1879; Leiper 1908; Baylis 1939; Hering-Hagenbeck and Boomker 2000). A very close relative of *T. tiara*, possibly a congeneric species, based upon Bayesian inference of phylogeny, has previously been recorded as encysted third stage larvae from the swim bladder of the African longfin eel *Anguilla mossambica* from the Eastern Cape in South Africa (Laetsch et al. 2012). The partial 28S rRNA sequence

(JF805627) of this specimen is identical (702 of 702 bp) to the corresponding base pairs of our slightly longer 28S rRNA sequence (990 bp), but no morphological description or taxonomic identification is provided by the authors (Laetsch et al. 2012). Moreover, our collected specimens differed in less than 1% (one of 681 bp) of their 18S rRNA fragments from *T. tiara* (JF934728), reported by the same authors from *Varanus indicus* in Australia (Laetsch et al. 2012). Nevertheless, as a result of the comparatively short fragment of 18S rRNA available and its high level of conservatism, in addition to the fact that we only have larval stages, we prefer to assign our specimens to *Tanqua* sp.



Figure 6: Third stage larval *Tanqua* sp. from the digestive tract of *Xenopus laevis*, photomicrographs. (a) general view; (b) anterior end of body, lateral view; (c) posterior end of body, lateral view. Scale bars: (a): 1 mm; (b), (c): 100 μ m

Unidentified nematode larvae sp. 1

Site of infection: Lungs and liver

Representative DNA sequences: 18S rRNA (MN526253)

Description

Second stage larva (Figure 7). Measurements based on 14 specimens. Minute nematodes, body thin, elongated, 583 μ m (530–619 μ m) long, 13 μ m (12–14 μ m) wide at midlength level. Stoma elongated, cylindrical, 15 μ m (13–18 μ m) long. Oesophagus narrow, oesophageal-intestinal junction poorly visible. Genital primordium not found. Tail short, with rounded end, 24 μ m (14–32 μ m) long.

Unidentified nematode larvae sp. 2

Site of infection: kidneys

Representative DNA sequences: 18S rRNA (MN526254)

Description

Second stage larva (Figure 7). Measurements based on eight specimens. Minute nematodes, body thin, elongated, 800 μ m (665–921 μ m) long, 15 μ m (13–17 μ m) wide at midlength level. Stoma elongated, cylindrical, 9 μ m (7–14 μ m) long. Oesophagus narrow, oesophageal-intestinal junction poorly visible. Nerve ring at 60 μ m (45–69 μ m) from anterior end. Genital primordium not found. Tail short, tapering, with rounded tip.

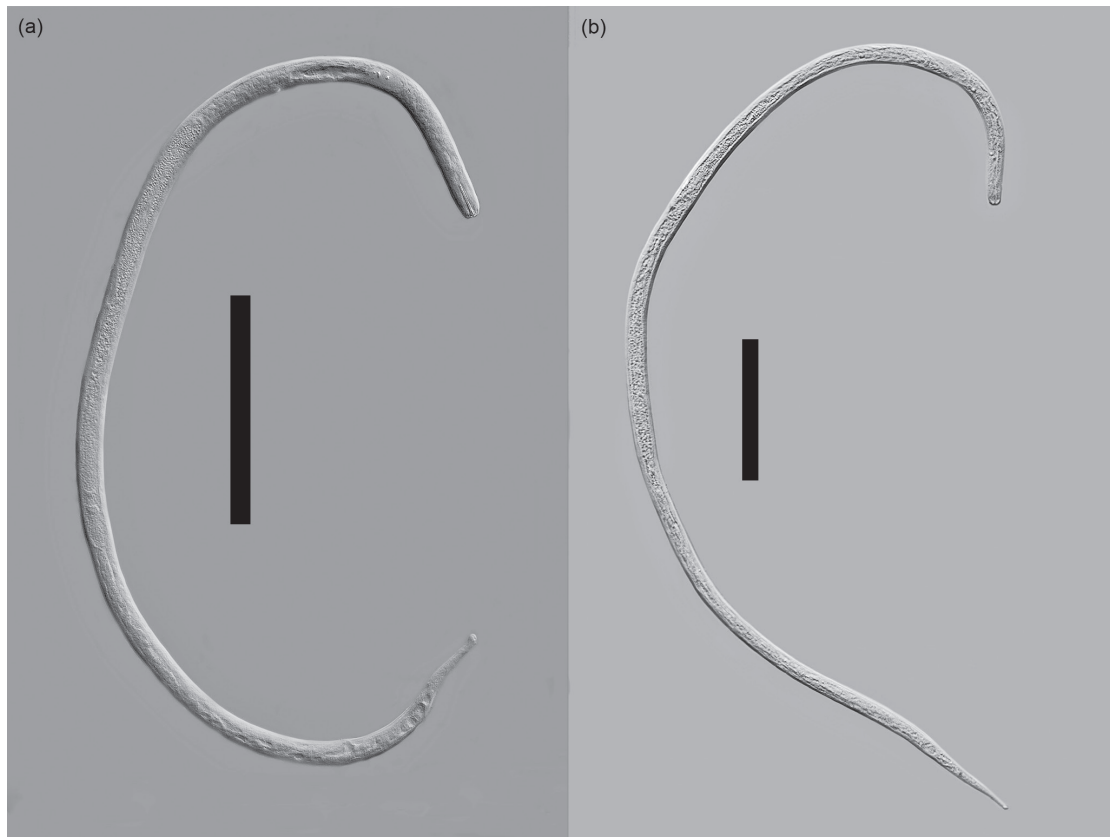


Figure 7: (a) Unidentified second stage nematode larvae sp. 1 from the lungs and liver of *Xenopus laevis*, photomicrographs. (b) Unidentified second stage nematode larvae sp. 2 from the kidneys of *Xenopus laevis*, photomicrographs. Scale bars: (a), (b): 100 μ m

Remarks for unidentified sp. 1 and 2

Two different species of larvae were recovered from the lungs and kidneys, respectively. The perceived differences in morphological characters (body length, stoma length) and the site of infection were also confirmed by the molecular data of the 18S rRNA alignment (22 out of 537 bp are different). Nevertheless, BLAST (Altschul et al. 1990) searching places both species closest to nematodes from the Family Thelastomatidae and the genera *Blattophila* Cobb, 1920 and *Travassosinema* (Rao 1958). Representatives of these taxa are commonly found in arthropods (insects and myriapods). Both species were found in high numbers in organs other than the digestive tract, accordingly post-cyclic or occasional infection is rather unlikely. In our opinion, they could well represent some primitive species of nematodes using *X. laevis* as an intermediate or paratenic host.

Role of *Xenopus laevis* in the transmission of nematode species

Of the seven species of nematodes reported here, subadult and ovigerous females were found for *Capillaria* sp.; adult males and females for *Falcaustra* sp.; third stage larvae for *Contraecaecum* sp., *Paraquimperia* sp. and *Tanqua* sp.; and second stage larvae of unidentified larvae sp. 1 and unidentified larvae sp. 2. Based on the available information on the life cycles, sites of infection and developmental stages of the retrieved nematodes,

we propose the role that *X. laevis* could play in their transmission (Figure 8).

Both direct and indirect life cycles have been described for fish-parasitising capillariids (Moravec et al. 1987; Køie and Nylund 2001). Because subadult and adult stages were found in the intestines, we consider *X. laevis* as a definitive host for the recovered *Capillaria* sp. Third stage larvae of *Contraecaecum* sp. were found encysted on the surface of the internal organs and in the body cavity, similar to previous findings of these nematodes in fish species (Moravec et al. 2016). Accordingly, we consider *X. laevis* as an intermediate and possible paratenic host for *Contraecaecum* sp. Because all the retrieved *Falcaustra* sp. specimens were adults and members of this genus usually make use of one intermediate host during their life cycle (Skrjabin et al. 1964), *X. laevis* could well be the definitive, or less likely paratenic, host for these nematodes. Third stage larvae of *Paraquimperia* sp. (known as a fish-parasitising genus) were found in the intestines of the studied frogs. Because of a lack of information on the life cycle of these nematodes, *X. laevis* could equally be considered as either a definitive or paratenic host for the recovered *Paraquimperia* sp. Third stage larvae of *Tanqua* sp. were observed encysted in intestines of *X. laevis*. Because the life cycle of this genus is poorly studied, *X. laevis* could either play a role as an intermediate or a paratenic host for the retrieved *Tanqua* sp. Both of the unidentified larval species were found unencapsulated and

in high numbers in blood-filled organs (lungs and kidneys). Therefore, these species most likely use *X. laevis* as an intermediate host.

Discussion

In total, approximately 1 400 specimens of seven species of nematodes from ten localities throughout South Africa were found parasitising *X. laevis*. The most widespread were encysted *Contracaecum* sp. third stage larvae, with a total of 183 specimens parasitising between 10 and 50% of the hosts at five of the studied localities. The other two species that were also recovered as third stage larvae, namely four *Paraquimperia* sp. and nine *Tanqua* sp. specimens, were recovered at just one locality each. Of the adult specimens, nine female *Capillaria* sp. were recovered from hosts at two localities in the Western Cape, whereas three females and four males of *Falcaustra* sp. were recovered from only one locality in the same area. The first species of unidentified second stage larvae was present in very high numbers (about a thousand larvae in total) in the lungs of half of the hosts at three localities. Conversely, approximately 150 specimens of the second species of unidentified second stage larvae were observed in the kidneys of only one frog.

Of these nematodes, only representatives of the genus *Contracaecum* have previously been reported from *X. laevis*, not in the native range, but in California and Chile (Kuperman et al. 2004; Castillo et al. 2017). The other six species are recorded from *X. laevis* for the first time herein,

although the possibility of associations with nematodes in the native range has been suggested by a few earlier reports (Thurston 1970; Cosgrove and Jared 1974; Brayton 1992). Surprisingly, this high number of novel parasite associations is reported despite more than 100 years of investigations and numerous parasitological surveys of *X. laevis* since the early 1900s (Cohn 1906; Metcalf 1923; Southwell and Kirshner 1937; Porter 1938; Sandon 1941; Price 1943; Nigrelli and Maraventano 1944; Elkan and Murray 1952; Dick 1959; Williams 1959; Vercammen-Grandjean 1960; Yeh 1960a, 1960b; Beverley-Burton 1963; Mettrick 1963; Manter and Pritchard 1964; Pritchard 1964; de Puytorac and Grain 1965; Thurston 1967; Dollfus 1968; Fischthal and Thomas 1968; Thurston 1970; Avery 1971; Macnae et al. 1973; Cosgrove and Jared 1974; Tinsley and Sweeting 1974; Tinsley and Wynne Owen 1975, 1979; Tinsley and Whitear 1980; Moravec and Cosgrove 1982; Wade 1982; Harris and Tinsley 1987; Ferguson and Appleton 1988a, 1988b; Jackson and Tinsley 1988; Kruger et al. 1991; King and van As 1992; Jackson and Tinsley 1995a, 1995b; Tinsley and Jackson 1995; du Preez et al. 1996; Tinsley 1996; Crous and du Preez 1997; Jackson and Tinsley 1997; King and van As 1997; Jackson and Tinsley 1998a, 1998b; Tinsley and Jackson 1998a, 1998b; King and van As 2000; Jackson and Tinsley 2001a, 2001b; Aisien et al. 2004; Bruňanská et al. 2012; Feldman and Ramirez 2014; Theunissen et al. 2014; Kruger and du Preez 2015; Svitin et al. 2018). We suggest that these new host-parasite associations could be a result of the

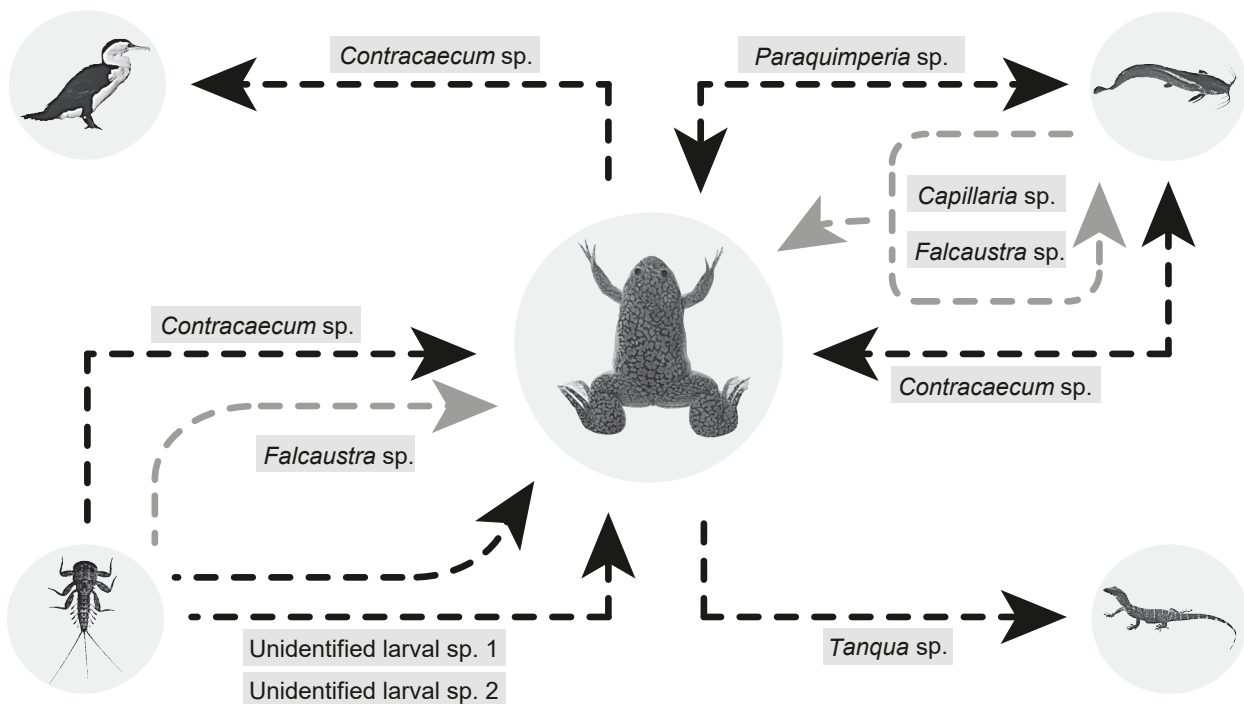


Figure 8: Hypothesised trophic transmission in a freshwater ecosystem of the seven nematode parasites recovered in the current study. *Xenopus laevis* (centre) acts as an intermediate or paratenic host for the larval stages of *Contracaecum* sp., *Paraquimperia* sp., *Tanqua* sp. and two other unidentified second stage larvae and is a possible definitive host for the adult stages of *Capillaria* sp. and *Falcaustra* sp. Other hosts include, from the top left corner in a clockwise direction, fish-eating birds, fish, semi-aquatic lizards and aquatic invertebrates. Arrow heads point in the direction of the predator

continuous domestic expansion (Measey and Davies 2011; de Villiers and Measey 2017; Measey et al. 2017) and deliberate translocation (van Sittert and Measey 2016) of *X. laevis* in its native range, with underrepresentation in the literature possibly heightened by the oversight of larval stages of nematodes in this frog in past investigations.

Unfortunately, as a result of a lack of molecular data, absence of clear morphological descriptions of larval stages and poorly studied life cycles of the recovered nematodes, we were not able to identify any of the collected nematodes to the species level and some not even to the family level. Indeed, even those specimens that were recovered in their adult stage, could only be identified to the genus level. This was true for *Capillaria* sp. that lacked males and *Falcaustra* sp. that lacked gravid females. In the case of the five species recovered as second or third stage larvae, it is almost impossible to distinguish larval stages of congeneric nematode species without applying molecular tools, because of high levels of morphological similarity at this stage of development (Anderson 2000). Unfortunately, very few species of nematodes parasitising ectothermic vertebrates from Africa have sequences available in GenBank and none of those available clearly correspond to the obtained sequences of the nematodes from the current study.

What is more, as a result of a lack of information on life cycles of African nematodes at large, we cannot specify the exact role of *X. laevis* in the transmission of the nematode species recovered during the current study. Nevertheless, in light of the data available on nematode life cycles, distribution, sites of infection and preferred host taxa from the region, we propose that *X. laevis* could be a definitive host for two species (*Capillaria* sp. and *Falcaustra* sp.), a paratenic host for three species (*Contraecum* sp., *Paraquimperia* sp. and *Tanqua* sp.) and an intermediate host for four species (*Contraecum* sp., *Tanqua* sp. and both species of unidentified larvae). These findings highlight the key role of *X. laevis* in the parasite dynamics of the freshwater ecosystems it forms part of. In many cases, it seems to act as a host for nematodes previously only associated with fish, as could be expected of an amphibian with a predominantly aquatic ecology (Elephant et al. 2000). This is illustrated by the past records of *Capillaria* sp. (Boomker 1994a; Moyo et al. 2009), *Contraecum* sp. (Whitfield and Heeg 1977; Mashego and Saayman 1981; Boomker 1982; van As and Basson 1984; Mashego 1989; Boomker 1994a, 1994b; Barson 2004; Barson and Avenant-Oldewage 2006; Barson et al. 2008; Boane et al. 2008; Moyo et al. 2009; Madanire-Moyo et al. 2010; Smit and Luus-Powell 2012; Sara et al. 2014; Mbokane et al. 2015; Moravec and van As 2015; Tavakol et al. 2015; McHugh et al. 2016; Moravec et al. 2016) and *Paraquimperia* sp. (Jackson 1978; Moravec et al. 2000), which hail from freshwater fish in Africa. Furthermore, previously undescribed routes of trophic nematode transmission via *X. laevis* to piscivorous birds, in the case of *Contraecum* sp. (Whitfield and Heeg 1977; Barson 2004), and semi-aquatic varanid lizards, in the case of *Tanqua* sp. (von Linstow 1879; Leiper 1908; Baylis 1939; Hering-Hagenbeck and Boomker 2000), are suggested.

Clearly, as has been shown for other invasive species (Dunn et al. 2012; Roy and Lawson Handley 2012;

Amundsen et al. 2013), the potential effects of *X. laevis* on freshwater ecosystems go beyond direct interactions. The current study demonstrates that *X. laevis* is a versatile parasite reservoir in its native range where it is a known domestic exotic, embarking on frequent pioneer and expansion events (Measey and Davies 2011; Measey et al. 2017). Potentially, it alters the parasite dynamics of not only nematodes associated with other amphibians, but also those of fish, reptile, bird and even invertebrate fauna, ultimately modifying trophic interactions at a large scale. Studies from the invasive range imply a similar role in the new habitats of *X. laevis*, where it has been shown to form novel associations with both larval nematodes and digeneans (Kuperman et al. 2004; Rodrigues 2014; Castillo et al. 2017).

Previous authors have warned that we remain ignorant of the native ecology of *X. laevis* to the detriment of its management elsewhere (Measey et al. 2012). The current study provides an example of how that might play out. Notably, third stage larvae of *Contraecum* have been reported before from *X. laevis* in the invasive range on two occasions (Kuperman et al. 2004; Castillo et al. 2017). Yet, because there had been no records of *Contraecum* associated with *X. laevis* in the native range before, the records in the invasive range were assumed to originate from the native fauna of the invasive regions. Whether this claim is true could probably only be ascertained by sufficient molecular data and morphological descriptions, both of which are lacking for *Contraecum* in both the native and invasive range.

When investigating the ecology of invasive species, the far-reaching effect of parasites should not be underestimated. It is specifically trophically transmitted parasites, of which all the recovered species are examples, that play the most prominent role in the alteration of networks post introduction (Amundsen et al. 2013). Introduced hosts could cause amplification and dilution effects for native parasite dynamics (Telfer and Bown 2012). For example, the arrival of another invasive amphibian in Australia, the cane toad, has been associated with lowered lungworm burdens in native toads, because they act as “dead-ends” for native parasites (Nelson et al. 2015; Selechnik et al. 2017).

Regrettably, these effects are not known for *X. laevis*, an invasive amphibian with a much greater global footprint than the cane toad. As a starting point to remedy this gap in our knowledge, the current study clearly shows the importance of the inclusion of molecular data, morphological descriptions and qualitative illustrations in parasitological surveys in Africa, even when reporting on the presence of larval stages. In addition, future investigations of *X. laevis* in its invasive range should not discount the insidious effects of parasites, both co-invading and newly associated, when determining the impact and subsequent management strategies of this globally invasive amphibian.

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