Co-introduction of ancyrocephalid monogeneans on their invasive host, the largemouth bass, *Micropterus salmoides* (Lacepède, 1802) in South Africa

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**A B S T R A C T**

Largemouth bass, *Micropterus salmoides* (Lacepède, 1802) were sampled from three provinces (Eastern Cape EC, North West NWP and KwaZulu-Natal KZN) in South Africa to assess for parasite diversity and community composition. Morphological evaluation of the sampled parasite specimens provided evidence for the first record of five monogeneans from the family Ancyrocephalidae: *Clavunculus bursatus* (Mueller, 1963), *Onchocleidus dispar* (Mueller, 1936), *Onchocleidus furcatus* (Mueller, 1937), *Onchocleidus principalis* (Mizelle, 1936) and *Syncleithrium fusiformis* (Mueller, 1934) from the African continent. Community composition differed between localities. *Clavunculus bursatus* were only sampled from the EC and KZN, *O. dispar* and *O. principalis* were only sampled from the EC, *O. furcatus* was only sampled from the NWP and KZN localities and *S. fusiformis* only from KZN. Prevalence was 100% at all localities. Data from this study support the enemy release hypothesis as many of the parasites reported from the native range of *M. salmoides* were not collected.

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1. Introduction

With the introduction of a species into a new environment, introduction of its symbionts and parasites can also occur (Taraschewski, 2006) if the parasites are able to overcome the barriers to introduction, establishment and spread (sensu Blackburn et al., 2011). With regard to fish parasites, the movement and introduction of their fish hosts typically results in four possible scenarios: enemy release, dilution, spillback and spill-over (Sheath et al., 2015). Enemy release is attained when, upon introduction into a new environment, the alien host loses some of its natural parasites. The result is that in some cases, introduced fishes may host fewer parasite species than in their native range (Petterson et al., 2016; Grendron et al., 2012; Roche et al., 2010; Torchin et al., 2003). Spillback occurs when parasites from native hosts transfer to the introduced alien host and there is increase in infection (Kelly et al., 2009). In some cases, spillback may result in dilution, when there is a decrease in the infection of the native hosts as aliens reduce transmission of parasites (Poulin et al., 2011; Keising et al., 2006). Finally, spill-over, also called pathogen pollution, might occur when an alien host introduces new parasites which then parasite novel hosts in the new range (Taraschewski, 2006; Daszek et al., 2000).

Parasites introduced with their host are known as co-introduced, while those introduced into a new environment with their alien host and then spill over to native hosts are known as co-invaders (Lymbery et al., 2014). Examples of co-introduced parasites of fishes that are of the monogeneans Onchocleidus dispar (Mueller, 1936) with the pumpkinseed fish Lepomis gibbosus (Linnaeus, 1758) into Norway (Sterud and Jorgensen, 2006) and Britain (Hockley et al., 2011), and Onchocleidus principalis (Mizelle, 1936) with largemouth bass into the British Isles (Maitland and Price, 2006; Daszek et al., 2000).

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In South Africa, fishes have been introduced since the 18th century for angling, aquaculture, biocontrol and as pets, and there are several examples of parasite co-introductions (Ellender and Weyl, 2014). Co-introductions are best described for cyprinid species such as C. caprio which are thought to have resulted in the co-introduction of Ichthyobodo necator Henneguy 1883, Chilodonella cyprini (Moroff, 1902), C. hexasticha (Kiernik, 1909), Apisomoma piscicola (Blanchard, 1885), Trichodina acuta (Kelly et al., 2009). In some cases, spillback may result in dilution, when there is a decrease in the infection of the native hosts as aliens reduce transmission of parasites (Poulin et al., 2011; Keising et al., 2006). Finally, spill-over, also called pathogen pollution, might occur when an alien host introduces new parasites which then parasite novel hosts in the new range (Taraschewski, 2006; Daszek et al., 2000).

2. Material and methods

2.1. Host and specimen collection

Micropterus salmoides were collected by angling from the Mook River (26° 41’3.60” S; 27°5’59.65” E) and Potchefstroom Dam (26°40’14.20” S; 27°05′46.94” E) in the North West Province (NWP) in October 2015; from Howison’s Poort Dam (33°23’10.07” S; 26°29′4.00” E) and Settlers Dam (33°24′41.67” S; 26°30′11.73” E) in the Eastern Cape (EC) in February 2016 and from Friedrichskron Dam (29°26′46.66” S; 30’33′38.67” E) in KwaZulu-Natal (KZN) in March 2016 (Fig. 1). Water temperature during sampling period ranged from 19.5 °C to 23.1 °C, with lowest values in KZN and highest in NWP.

Fish were kept alive in keep-nets or aerated containers until euthanasia by percussive stunning and cervical vertebrae dislocation was performed. All fish were measured for standard length (SL) in mm and weighed (W) to the nearest in gram. A full parasitological screening was performed following the techniques described by Truter et al. (2016) and McHugh et al. (2016) and parasite specimens were removed from the fins, gills and body cavity and the total number of all gill parasites was counted. This study received the relevant ethical approval (North-West University ethics approval no: NWU-00439-16-S5).

2.2. Specimen preparation and morphological analysis

All monogenean specimens collected were mounted on a microscopy slide and fixed in glycerine ammonium picrate for morphological analysis (Malmberg, 1970). Parasites were examined (under 40×, 60× and 100× oil immersion magnification) using a Nikon Eclipse 80i compound microscope. Morphometrics and images were obtained using a Nikon DS-Fi1 camera mounted on the compound microscope and NIS-Element v4 software. Identification of individual specimens was done comparing morphology and measurements of taxonomic important structures, hamuli and male copulatory organ (MCO), to literature (Beverley-Burton and Suriano, 1980; Beverley-Burton, 1986; Wheeler and Beverley-
Marginal hook arrangement for *Onchocleidus* spp. follows that of Wheeler and Beverley-Burton (1989) and Clavunculus and Synceleithrium that of Mizelle (1940). Mean and range are given in micrometers for all structures measured, unless otherwise indicated.

### 2.3. Statistical analysis

Prevalence, mean intensity and intensity of infection were calculated according to Bush et al. (1997). GraphPad Prism 5 software was used to perform statistical analysis and comparisons of data collected from each locality. The D’Agostino & Pearson omnibus normality test was used to test for normality of fish size (SL) and intensity of parasite infection of each locality in relation to one another. One-way analysis of variance (ANOVA) was performed with Tukey’s multiple comparison test as a post test, if data were parametrically distributed. For non-parametric data sets, the Kruskal-Wallis test was performed with Dunn’s multiple comparison test as a post-hoc test. A $p<0.05$ was considered as significant. Spearman’s rank correlation analysis was used to determine if there was a correlation between fish size and parasite load.

### 3. Results

#### 3.1. General

The gills of all host specimens were infected with monogeneans. Table 1 summarizes size of fish and monogenean ecological parameters. Intensity of infection from hosts in the NWP was significantly lower from those in the EC and in KZN ($p<0.0001$).

The size of hosts examined from KZN was significantly larger ($p<0.05$) than those collected from the EC and NWP. A strong correlation was found between log-transformed data of fish size and intensity of parasite infection for NWP ($r = 0.81$), intensity of infection increases with fish size. Fish from KZN ($r = 0.06387$) and

### Table 1

Summary of fish biometrics and ecological parameters of monogenean parasites load. $n$ – number of fish studied; Mean SL – mean standard length; Mean IF – mean intensity of infection.

|                | n  | Mean SL ±SD | Prevalence (%) | Mean IF |
|----------------|----|-------------|----------------|--------|
| North West     | 13 | 165.8 ± 79.24 | 100            | 32 (1–86) |
| Eastern Cape   | 30 | 228.1 ± 39.74 | 100            | 448 (194–1668) |
| KwaZulu-Natal  | 15 | 260.2 ± 34.66 | 100            | 399 (60–736) |

Fig. 1. Map of the sampling localities in the Eastern Cape, Kwazulu-Natal and North West Provinces of South Africa.
EC \((r = 0.01876)\) had a weak correlation between log-transformed data for fish size and intensity of parasite infection, thus the size of the fish did not affect the intensity of infection.

### 3.2. Parasite community

Parasites of two nematode, one protozoan and five monogenean species were sampled. The nematodes comprised larval Contracaecum sp. present in low numbers on specimens in the EC \((n = 4)\) and KZN \((n = 2)\) populations and a larval Spinitectus sp. from the NWP \((n = 1)\). Seven Trichodina sp. specimens were also sampled from the EC populations. Of the 1986 monogenean parasites counted, a sub-sample of 816 specimens was collected. These were identified as five species belonging to three different genera of Ancyrocephalidae: Clavunculus bursatus (Mueller, 1936) (Fig. 2A–B), Onchocleidus dispar (Mueller, 1936) (Fig. 2C–D), Onchocleidus furcatus (Mueller, 1937) (Fig. 2E–H), Onchocleidus principalis (Mizelle, 1936) (Fig. 3A–C) and Synlechotrema fusiformis (Mueller, 1934) (Fig. 3D–E). Overall monogenean species richness was higher in KZN \((3 \times 2)\) and the EC \((3 \times 2)\) species) than in the NWP \((1 \times 2)\). As the nematode and protozoan parasites could not be identified to species level, they were elided for subsequent analyses.

Monogenean parasite community composition and abundance, in percentage, of the parasite species at each locality is presented in Fig. 4. Synlechotrema fusiformis \((8 \%)\) from KZN were the least abundant species, followed by C. bursatus \(3 \%(KZN)\) and 4\% \((EC)\) and O. dispar \(9 \%(EC)\). Onchocleidus furcatus \(100 \%(NWP)\) and 89\% \((KZN)\) and O. principalis \(86 \%(EC)\) were the most abundant species and were not found in association with each other, but dominating in their respective geographic region in South Africa.

### 3.3. Morphology

Family Ancyrocephalidae Bychowsky and Nagibina, 1978.

Genus Clavunculus Mizelle, Stokely, Jaskoski, Seamster and Monaco, 1956.

Clavunculus bursatus (Mueller, 1936) (Fig. 3A–B).

**Type host:** Micropterus salmoides.

Other hosts: Lepomis cyanellus; L. macrochirus; L. marginatus; L. megalotis; L. microlophus; Micropterus dolomieui; M. punctulatus.

**Type locality:** Florida, USA.

Material examined. Fifteen specimens collected from M. salmoides caught in the Mooi River \((26'41"3.60'"S; 27'5"59.65'"E)\) and Potchefstroom Dam \((26'40"14.20'"S; 27'5"46.94'"E)\) and three specimens collected from M. salmoides in the Friedrichskron Dam \((29'26"46.66'"S; 30'33"38.76'"E)\) were studied. Voucher material (acc. no. NMB P 444) are deposited in the parasite collection of the National Museum, Bloemfontein (NMB).

**Description:** Two pairs of hamuli, dissimilar in shape and size (Fig. 2C); dorsal bar straight with knobbed ends, ventral bar bow shaped. Marginal hooks with ovate elliptical base, slender shaft and sickle shaped hook, similar in shape, pairs I – II similar in size, pairs III – VII slightly longer, distributed along anterolateral margins of haptor. Male copulatory complex (Fig. 2D) comprise of sclerotized straight penis, thick at base, sclerotized accessory piece with elongate handle and distal ring through which penis passes. Vagina not observed.

**Remarks:** Compared to O. dispar populations from native regions, individuals from non-native region (present study) has shorter ventral bar length and smaller marginal hooks than those reported by Beverley-Burton and Suranon (1980). All other characters were within range of measurements given from the different hosts (see Table 1).

**Onchocleidus furcatus** (Mueller, 1937) (Fig. 2E–H).

**Type host:** Micropterus salmoides.

Other hosts: Lepomis cyanellus; L. macrochirus; L. marginatus; L. megalotis; L. microlophus; Micropterus dolomieui; M. punctulatus.

**Type locality:** Florida, USA.

Material examined. Fifteen specimens collected from M. salmoides caught in the Howison’s Poort Dam \((33'23"10.07'"S; 26'29"4.00'"E)\) and four specimens from M. salmoides caught in the Settlers Dam \((33'24"41.67'"S; 26'30"11.73'"E)\). Voucher material (acc. no. NMB P 443) are deposited in the parasite collection of the National Museum, Bloemfontein.

**Description:** Two pairs of hamuli, dissimilar in shape and size (Fig. 2C); dorsal bar straight with knobbed ends, ventral bar bow shaped. Marginal hooks with ovate elliptical base, slender shaft and sickle shaped hook, similar in shape, pairs I – II similar in size, pairs III – VII slightly longer, distributed along anterolateral margins of haptor. Male copulatory complex (Fig. 2D) comprise of sclerotized straight penis, thick at base, sclerotized accessory piece with elongate handle and distal ring through which penis passes. Vagina not observed.

**Remarks:** Morphometrics of specimens from South African were within the same ranges as those parasitising M. punctulatus and M. salmoides from native regions reported by Mizelle (1940) and Beverley-Burton (1986), except in that the male copulatory complex of the South African specimens are larger in size (see Table 3). Genus Onchocleidus (Mueller, 1936).

**Onchocleidus dispar** (Mueller, 1936) (Fig. 2C–D).

**Type host:** Lepomis gibbosus.

Other hosts: Archoplites interruptus; Lepomis auritus; L. cyanellus; L. gulosus; L. humulis; L. macrochirus; Micropterus dolomieui; M. salmoides.

**Type locality:** Constantia, New York, USA.

Material examined. Three specimens collected from M. salmoides caught in the Howison’s Poort Dam \((33'23"10.07'"S; 26'29"4.00'"E)\) and four specimens from M. salmoides caught in the Settlers Dam \((33'24"41.67'"S; 26'30"11.73'"E)\). Voucher material (acc. no. NMB P 443) are deposited in the parasite collection of the National Museum, Bloemfontein.
Fig. 2. *Clavunculus bursatus* (Mueller, 1936) haptoral hooks (A), male copulatory organ (B); *Onchocleidus dispar* (Mueller, 1936) haptoral hooks (C); male copulatory organ (D); *Onchocleidus furcatus* (Mueller, 1937) haptoral hooks (E); male membrane on ventral bar (F), copulatory organ (G), vagina (H). Scale: A–E, G–H: 50 μm; F: 10 μm.
**Syncleithrium fusiformis** (Mueller, 1934) Price, 1967 (Fig. 3D–E).

**Type host:** *Micropterus dolomieui*.

**Other hosts:** *Leponis cyanellus;* *L. gulosus;* *L. macrochirus;* *L. megalotis;* *M. punctulatus;* *M. salmoides.*

**Type locality:** Syracuse, New York; London, Ohio, USA.

**Material examined:** Seventeen specimens collected from *M. salmoides* caught in the Friedrichskron Dam (29°26′46.66″ S; 30°33′38.76″ E) were studied. Voucher material (acc. no. NMB P 446) are deposited in the parasite collection of the National Museum, Bloemfontein.

**Description:** Large gyrodactyloid with characters of genus. Haptor not wider than body. Marginal hooks distributed in typical ancyrocephalid pattern, as described above. Marginal hooks similar in shape, with base, elongate shaft and hook, slightly dissimilar in size. Hamuli and bars in central region of haptor ventral and dorsal bars projecting laterally beyond haptoral margin (Fig. 3D). Hamuli robust, distinguishable — dorsal hamuli long inner root, compared to that of ventral hamuli. Transverse bars articulate with each other forming single supporting plate for hamuli. Ventral bar centrally horizontal, V-shaped, with oblique distal struts, dorsal bar a solid, shield-like plate, wider than long, central portion may be absent. Male copulatory complex (Fig. 3E) comprising of well sclerotized penis with shaft and curved distal point and a lightly sclerotized base, accessory piece sclerotized with distal limb characterized by bifid tip which guides distal extremity of penis. Accessory piece attached to penis by strands of muscle. Vagina sclerotized, submarginal, left side of body.

**Remarks:** The *Syncleithrium fusiformis* collected from South African population a membrane on the ventral bar can be present or absent (Fig. 3B). Marginal hooks similar in shape, with base, elongate shaft and hook, slightly dissimilar in size. Hamuli and bars in central region of haptor ventral and dorsal bars projecting laterally beyond haptoral margin (Fig. 3D). Hamuli robust, distinguishable — dorsal hamuli long inner root, compared to that of ventral hamuli. Transverse bars articulate with each other forming single supporting plate for hamuli. Ventral bar centrally horizontal, V-shaped, with oblique distal struts, dorsal bar a solid, shield-like plate, wider than long, central portion may be absent. Male copulatory complex (Fig. 3E) comprising of well sclerotized penis with shaft and curved distal point and a lightly sclerotized base, accessory piece sclerotized with distal limb characterized by bifid tip which guides distal extremity of penis. Accessory piece attached to penis by strands of muscle. Vagina sclerotized, submarginal, left side of body.

**Remarks:** The *Syncleithrium fusiformis* collected from South African population a membrane on the ventral bar can be present or absent (Fig. 3B). Marginal hooks similar in shape, with base, elongate shaft and hook, slightly dissimilar in size. Hamuli and bars in central region of haptor ventral and dorsal bars projecting laterally beyond haptoral margin (Fig. 3D). Hamuli robust, distinguishable — dorsal hamuli long inner root, compared to that of ventral hamuli. Transverse bars articulate with each other forming single supporting plate for hamuli. Ventral bar centrally horizontal, V-shaped, with oblique distal struts, dorsal bar a solid, shield-like plate, wider than long, central portion may be absent. Male copulatory complex (Fig. 3E) comprising of well sclerotized penis with shaft and curved distal point and a lightly sclerotized base, accessory piece sclerotized with distal limb characterized by bifid tip which guides distal extremity of penis. Accessory piece attached to penis by strands of muscle. Vagina sclerotized, submarginal, left side of body.

**Type locality:** Salt Fork of the Big Vermillion River, Homer, Illinois, USA.

**Material examined:** Fifteen specimens collected from *M. salmoides* caught in the Settlers Dam (33°24′41.67″ S; 26°30′11.73″ E) were studied. Voucher material (acc. no. NMB P 445) are deposited in the parasite collection of the National Museum, Bloemfontein.

**Description:** Two pairs of hamuli similar in shape and size (Fig. 3A); dorsal bar curved with knobbed ends, ventral bar slightly curved with membrane present or absent (Fig. 3B). Marginal hooks similar in shape, pairs I — II similar in size, positioned directly posterior to dorsal hamuli and anterior to ventral hamuli, respectively, pairs III — VII slightly longer, distributed along anterolateral margins of haptor. Male copulatory complex comprise of sclerotized helical with 6 — 9 turns, sclerotized accessory piece with elongate handle, bifid distally (Fig. 3C). Vagina unsclerotized.

**Remarks:** *Oncholeidus principalis* found in present study is morphometrical and morphological similar to previously descriptions of this species (see Table 2), except that in the South African population a membrane on the ventral bar can be present or absent (Fig. 3B) where previously no mention was made of a membrane (Wheeler and Beverley-Burton, 1989).
Africa is morphological and morphometrically similar to those previously described (see Table 3).

4. Discussion

Until recently seven Ancyrocephalid species: Actinocleidus fergusoni Mizelle, 1938, Clavunculus bursatus, O. dispar, O. furcatus, O. helicis Mueller, 1936 O. principalis and S. fusiformis were known to parasitise M. salmoides in their native range (Mizelle and Cronan, 1943; Mueller, 1937; Mizelle and Crane, 1964; Hargis, 1953; Rawson and Rogers, 1972; Molnar et al., 1974; Joy, 1984; Hoffman, 1999). Galaviz-Silva et al. (2016) commutated this to eight, when reporting M. salmoides as a new host of Clavunculus bifurcatus (Mizelle, 1941). Five of these eight ancyrocephalid species were sampled from M. salmoides in South Africa during the present study. As these parasites are common in centrarchid fishes in their native range, they were most likely co-introduced with M. salmoides or the other centrarchid fishes that were introduced into South Africa between 1928 and 1980. Interestingly, the results of the current study (Fig. 4) also correspond to Mizelle and Crane (1964) observations that no more than four of the seven known species occur at any one locality.

Studies yielding similar results in parasite community structure reported here, include that of Joy (1984) reporting four ancyrocephalids with a low frequency of C. bursatus and S. fusiformis with O. furcatus and O. helicis as the dominant species from M. salmoides collected in Beech Fork Lake, West Virginia. Mizelle and Crane (1964) and Rawson and Rogers (1972) reported a parasite community comprising of all species present in this study with the exclusion of O. dispar. The former reported fluctuation in proportions of species in parasite population between summer and autumn, respectively, from the California pond: C. bursatus (50% and absent), O. furcatus (23% and 32%), O. principalis (60% both seasons) and S. fusiformis (3% and 7%). Similarly, the latter reported O. furcatus and O. principalis dominating on the same host in association with low numbers of C. bursatus and S. fusiformis from the Walter F. George Reservoir, Alabama, USA. Cloutman (1975) also reported the same four monogenean species (excluding O. dispar) and A. ureterocoetes parasitising M. salmoides from Lake Fort Smith, Arkansas. All of the aforementioned literature reflects seasonal differences in the abundance of parasite community from a single location studied. In the study of Galaviz-Silva et al. (2016) the parasite community of M. salmoides from five localities were investigated. Of the six monogenean species found to parasitise M. salmoides, the presence of four ancyrocephalids correspond with the present study. Clavunculus bursatus were found to parasitise between 60% and 86.6% of hosts at all studied locations in relative high abundances Onchocleidus dispar, O. principalis and S. fusiformis occurred only on a few hosts from one locality in relative low numbers. From above mentioned studies, it is clear that changes in season, reflected in the changes of water temperature, have an influence on the abundance or reproduction of these ancyrocephalids. Predominantly parasite community structure, in terms of abundance and not richness, changed. Although investigation of parasite fauna for the selected localities in the present study were not performed throughout all seasons, it is interesting that such distinct community structures were found from each locality despite the relevantly low fluctuation in water temperature. This

Fig. 4. Composition and abundance of monogenean species at each sampling locality.
### Table 2
Morphometrics of *Onchocleidus dispar*, *O. furcatus* and *O. principalis*, from gills of *Micropterus salmoides* in South Africa.

| Onchocleidus dispar | Onchocleidus furcatus | Onchocleidus principalis |
|---------------------|-----------------------|-------------------------|
| **Host(s)**         | M. salmoides Tennessen, USA | M. dolomieu Ontario, Canada | L. gibbosus Ontario, Canada |
| **Locality**        | M. salmoides South Africa | M. salmoides - Tennessee, USA | M. salmoides - Tennessee, USA |
| **Body length**     | 650 (540–732)          | 410 (320–596)           | 352 (238–423)           |
| **Body width**      | 86 (84–108)            | 100 (90–111)            | 128 (100–128)           |
| **Haptor length**   | 57 (72–86)             | 75 (50–100)             | 67 (58–67)              |
| **Haptor width**    | 71 (116–132)           | 125 (100–150)           | 82 (68–86)              |
| **Pharynx**         | 43 (40–44)             | 30 (28–40)              | 25 (22–30)              |
| **Dorsal hamuli**   | 69 (51–54)             | 71 (60–64)              | 74 (43–79)              |
| **Aperture length** | 34 (31–35)             | 1 (1–2)                 | 43 (1–4)                |
| **Accessory piece** | 14 (13–16)             | 17 (14–17)              | 17 (12–19)              |
| **Penis length**    | 26 (20–30)             | 30 (26–30)              | 36 (31–36)              |
| **Ventral hamuli**  | 36 (32–34)             | 40 (35–36)              | 33 (31–33)              |
| **Inner root length** | 27 (25–27)           | 32 (28–32)              | 27 (25–27)              |
| **Outer root length** | 34 (31–35)           | 1 (1–2)                 | 2 (1–3)                 |
| **Dorsal bar length** | 23 (25–27)            | 28 (26–28)              | 27 (25–27)              |
| **Dorsal bar median** | 5 (4-6)               | 4 (3-4)                 | 5 (4-7)                 |

**Table Notes:**
- *Mizelle and Cronan, 1943* (n = 1)
- *Hanek and Fernando, 1972* (n = 10)
- *Beverly-Burton & Suranio, 1980* (n = 20)
- *Mizelle, 1940* (n = 8)
- *Beverly-Burton, 1989* (n = 13)
- *Wheeler, 1940* (n = 4)
- *Beverly-Burton, 1989* (n = 10)

**Average, minima and maxima are given.**

**15 specimens from North West and 3 form KwaZulu-Natal were examined.**

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might be an example of interspecific competition between species for a specific niche on the host in the novel environment (Cloutman, 1975). Further investigation is needed. Species richness for monogeneans in general was lower in South Africa (n = 5) than in North American *M. salmoides* populations with a total of 13 monogenean species reported from its native range (Hoffman, 1999; Galaviz-Silva et al., 2016). The lower abundance and species richness in South Africa therefore supports the enemy release
hypothesis (Sheath et al., 2015). With regard to the ancyrocephalid communities in particular, the species composition on the M. salmoides host populations is also less diverse (50%) than in North American populations (n = 10) and is comprised of those species capable of overcoming barriers set by introduction into a novel environment, supporting enemy release (Lymbery et al., 2014).

Differences between studied localities in South Africa could also be a consequence of the introduction from populations which might simply reflect the parasite community structure in the native region from where they were sourced (Mizelle and Crane, 1964). Although evidence is scant, the possibility of multiple M. salmoides or cross-infection from other centrarchid species introductions cannot be ignored. Although C. bursatus, O. principals and S. fusiformis are extremely host specific, only parasitising M. salmoides even in the presence of other potential centrarchid hosts, O. dispar and O. furcatus are less host specific, having been reported to also parasite Lepomis cyanellus Rafinesque, 1819, L. macrochirus and Pomoxis nigromaculatus (Collins and Janovy, 2003). As a result, the potential for spill-over to native fishes and the spill-back to other introduced centrarchids requires further investigation.

In conclusion, this study presents the first report of C. bursatus, O. dispar, O. furcatus, O. principals, S. fusiformis from introduced alien M. salmoides on the African continent. Furthermore, these parasites are all considered as co-introduced with largemouth bass. In revisiting invasion hypotheses, our results support the enemy release hypothesis in that the invasive largemouth bass have lost some of its natural parasites, but due to the paucity of our knowledge on the parasites of the native fishes from the regions studied it is not clear whether spillback, dilution or spill-over have occurred.

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Table 3

| Clavunculus bursatus |  | Syncelethrium fusiformis |
|----------------------|-------------------------|-------------------------|
| Body length | 820 (646–1006) | 483 (270–910) |
| Body width | 328 (172–405) | 132 (68–180) |
| Haptor length | 216 (144–270) | 89 (85–97) |
| Pharynx length | 111 (61–130) | 35 (29–43) |
| Anchor length | 27 (22–30) | 51 (44–51) |
| Point length | 7 (6–9) | 26–27 |
| Shaft length | 24 (23–28) | – |
| Inner root length | 6 (4–7) | – |
| Outer root length | 2 (1–3) | – |
| Aperture length | 14 (13–15) | – |
| Dorsal bar length | 19 (15–22) | 46 (45–47) |
| Ventral bar length | 5 (4–6) | 42–44 |
| Marginal hooks | – | – |
| Male copulatory complex | – | – |
| vagina length | – | – |
| vagina width | – | – |
| Penis length | 41 (39–46) | 49 (38–55) |
| Accessory piece | 27 (25–28) | 31 (27–34) |
| Host (s) | M. punctulatus | M. salmoides |
| Geographic locality | Tennessee, USA | South Africa |

Average, minima and maxima is given.

Only 12 haptors and complete specimens could be studied.
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