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# **Research Paper**

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Author for correspondence: L.R. Smales, E-mail: l.warner@cqu.edu.au A new species of *Pseudoacanthocephalus* (Acanthocephala: Echinorhynchidae) from the guttural toad, *Sclerophrys gutturalis* (Bufonidae), introduced into Mauritius, with comments on the implications of the introductions of toads and their parasites into the UK

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# Abstract

*Pseudoacanthocephalus goodmani* n. sp. is described from faecal pellets collected from *Sclerophrys gutturalis* (Power, 1927), the guttural toad. The species is characterized by a suite of characters, including a proboscis armature of 14–18 longitudinal rows of 4–6 hooks with simple roots, lemnisci longer than the proboscis receptacle, equatorial testes, a cluster of elongated cement glands and eggs without polar prolongations of the middle membrane 72.6–85.8 long. The toad had been accidentally translocated from Mauritius to the UK in a tourist's luggage and survived a washing machine cycle. The guttural toad was introduced into Mauritius from South Africa in 1922 and the cane toad, *Rhinella marina* (Linneaus, 1758), from South America, between 1936 and 1938. It seems most likely, therefore, that *P. goodmani* was introduced, with the guttural toad, from South Africa. The cane toad is host to the similar species, *Pseudoacanthocephalus lutzi*, from the Americas, but *P. lutzi* has not been recorded from places where the cane toad has been introduced elsewhere. Clearly, the guttural toad is a hardy and adaptable species, although it seems unlikely that it could become established in Northern Europe. Nevertheless, any accidental translocation of hosts poses the potential risk of introducing unwanted pathogens into the environment and should be guarded against.

# Introduction

Establishing the validity of the acanthocephalan genus *Pseudoacanthocephalus* Petrochenko, 1956 (Echinorhynchidae), parasitic in amphibians and reptiles, has been problematic. The importance of the characters Petrochenko (1956, 1958) used to separate species of the genus *Acanthocephalus* from those of *Pseudoacanthocephalus* have been a matter for debate (see, for example, Kennedy, 1982). Nevertheless, species from terrestrial hosts have continued to be assigned to the genus *Pseudoacanthocephalus* and species from aquatic hosts assigned to the sister genus *Acanthocephalus* Koelreuther, 1771. Recently, Amin *et al.* (2008, 2014) and Tkach *et al.* (2013) reviewed the genus *Pseudoacanthocephalus*, discussed its validity and presented keys to its species. Tkach *et al.* (2013) also provided some preliminary molecular sequence data and analyses.

The guttural toad, *Sclerophrys gutturalis* (Power, 1927) is widespread throughout much of sub-Saharan Africa (Channing, 2001) and is quite distinctive due to its loud calls. Individuals can attain a comparatively large size, with a snout-to-vent length of up to 120 mm (Spawls *et al.*, 2006). *Sclerophrys gutturalis* is common due to its adaptability to a range of habitats including savannah, agricultural land and even garden ponds (Channing, 2001) and is listed by the International Union for the Conservation of Nature (IUCN) as of Least Concern (IUCN SSC Amphibian Specialist Group, 2016). The introduction of guttural toads to Mauritius occurred in 1922 as a method of biocontrol for the cane beetle *Phyllophaga smithi* (Arrow, 1912) (see Cheke & Hume, 2008). Toads were then collected from Mauritius in 1927 to act as a form of biocontrol against mosquito larvae in Réunion, in an attempt to control malaria (Cheke & Hume, 2008). Recent research has identified that the toads originally introduced to these two islands came from source populations in South Africa (Telford *et al.*, 2019).

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Following a series of remarkable events, specimens of an acanthocephalan emerged alive from a female guttural toad that had arrived in the UK as a stowaway from Mauritius and subsequently entered the care of the Cambridge and Peterborough Amphibian and Reptile Group (CPARG). The acanthocephalans were found to be a new species of *Pseudoacanthocephalus*, which is described in the results section. The implications of the introduction of the guttural toad into the UK, with its parasites, are considered.

## **Materials and methods**

A female guttural toad, *S. gutturalis* (fig. 1), found its way into Cambridgeshire, UK, in October 2015, within the luggage of tourists who had been visiting Mauritius. The toad quickly found a temporary home with one of the authors (S.J.R.A. of CPARG). It was during this time that the acanthocephalans were collected and submitted for further analysis.

A total of 11 male and 16 female worms were collected on three or four occasions, from faecal pellets left by the guttural toad, fixed in formalin and stored in 70% ethanol. The acanthocephalans were cleared in lactophenol prior to examination as temporary wet mounts using an Olympus BH-2 compound microscope (Olympus, Japan). Measurements in micrometres, unless otherwise stated, were made using an ocular micrometre and are presented as the range, followed by the mean in parentheses, where three or more measurements were taken. Drawings were made with the aid of a drawing tube. Type specimens were deposited in the Natural History Museum, London (NHMUK) and voucher specimens in the South Australian Museum, Adelaide (SAMA).

### Results

## Pseudoacanthocephalus goodmani n. sp. (figs 2 and 3)

## Description

*General.* Echinorhynchidae. Trunk medium-sized, smooth, more or less cylindrical, widest anteriorly. Females larger than males. Lacunar system comprising two longitudinal lateral canals with numerous small reticulate canals forming a network. Proboscis cylindrical, armed with 14–18, usually 14, longitudinal alternating rows of 4–6 hooks each, usually five, with simple roots. Hooks 1 and 5 usually smaller than hooks 2–4. Neck short, broader at base. Proboscis receptacle double-walled, attached to the base of proboscis. Cerebral ganglion at base of proboscis receptacle. Lemnisci digitiform, longer than proboscis receptacle. Genital pore subterminal in males and females.

*Male* (based on five specimens) (fig. 2a–d). Trunk 6–11 (8.4) mm long, 1020–1632 (1254) at widest part. Proboscis 302–629 (473) long, 221–268 (256) wide. Hook blades, measurements of two rows, from three proboscides. Blades proboscis 1 (1) 86, 93; (2) 93, 96; (3) 73, 83; (4) 73, 69. Proboscis 2 (1) 46, 66; (2) 53, 72; (3) 66, 69; (4) 66, 66; (5) 66, 63. Proboscis 3 (1) 83, —; (2) 93, 58; (3) 99, 60; (4) 102, 66; (5) 96, 63; (6) 83, 60. Roots proboscis 1 (1) 43, 36; (2) 50,53; (3) 53, 63; (4) 56, 50. Proboscis 2 (1) 36, 36; (2) 53, 43; (3) 53, 50; (4) 50, 43; (5) 50; 63. Neck 147–235 (206) long, 389–489 (438) wide. Proboscis receptacle 737–850 (798) long, 255–402 (306) wide. Lemnisci 703–1445 (1166) long, 200 wide. Testes equatorial, ovoid, tandem, contiguous; anterior testis 503–603 (576) long, 355–408 (391) wide; posterior testis 516–629 (580) long, 295–482 (389) wide. Cement glands six in



Fig. 1. The guttural toad (Sclerophrys gutturalis) that made its way to Cambridge.

compact cluster of two tiers, elongate, 900–1750 (1360) long, 60–300 (144) wide; two cement ducts overlapping Saefftigen's pouch, Saefftigen's pouch 637, 740 long (two measurements). Bursa not extended.

Female (based on ten specimens) (fig. 3a-e). Trunk 14-19 (16.5) mm long, 1292-1870 (1579) wide. Proboscis 502-605 (556) long, 235-402 (290) wide. Hook measurements from three rows, two proboscides. Blades proboscis 1 (1) 53, 99, -; (2) 79, 99, 102; (3) 86, 106, 106; (4) 83, 99, 93; (5) 56, -, 73. Proboscis 2 (1) 86, 99, 93; (2) 109, 99, 93; (3) 103, 99, 92; (4) 93, 96, 73; (5) -, 93. Roots proboscis 1 (1) 50, 51; (2) 45, 45; (3) 50, 45; (4) 40, 50; (5) 38, 35. Proboscis 2 (1) 45, 45; (2) 50, 40; (3) 45, 45; (4) 45, 40; (5) 35, 30. Neck 170-368 (243) long, 442-603 (529) wide. Proboscis receptacle 782-1122 (989) long, 153-680 (343) wide. Lemnisci 1105-1608 (1472) long, 250, 290 wide (two measurements). Reproductive system from anterior edge of uterine bell to genital pore 935-1870 (1325) long. Vagina with two sphincters, the internal sphincter well developed. Uterine wall thick and uterine bell glands many. Eggs ovoid, without polar prolongation of fertilization membrane, 72.6-85.8 (76.3) long, 23.1-26.4 (26.0).

#### Taxonomic summary

*Type host.* Guttural toad *S. gutturalis* (Power, 1927) (Bufonidae).

Site of infection. Digestive system.

Type locality. Mauritius.

*Prevalence and intensity.* One animal examined with 27 worms.

*Specimens deposited.* Holotype male NHMUK 2019.11.12.1, allotype female NHMUK 2019.11.12.2, paratypes NHMUK 2019.11.12.3–20 in NHMUK; vouchers one male, one female, two anterior ends female, SAMA AHC48865 in SAMA.

*Etymology.* The species name is given in recognition of the enthusiasm and commitment of Mark Goodman (CPARG) to the conservation of British herpetofauna.

## Remarks

The new species is accommodated within the genus *Pseudoacanthocephalus* because specimens have the generic









(c)

**Fig. 3.** *Pseudoacanthocephalus goodmani* n. sp. female from *Sclerophrys gutturalis* in Mauritius. (a) Proboscis; (b) reproductive apparatus with uterine bell, uterus and vagina; (c) entire specimen, lateral view; (d) anterior end, lateral view; (e) egg. Scale bars: (a, b) 200 µm; (c) 2 mm; (d) 500 µm; (e) 25 µm.

characters of an aspinose cylindrical trunk, a cylindrical proboscis with hooks arranged quincuncially, a short neck, a cluster of cement glands, eggs without polar prolongation of the fertilization membrane and are parasitic in a toad (Petrochenko, 1958; Golvan, 1969). *Pseudoacanthocephalus goodmani* n. sp. does not, however, correspond to any species listed in the most recent key to the species (Tkach et al., 2013). In having a proboscis hook formula of 14–18, usually 14 longitudinal rows of 4–6, usually five hooks and six cement glands. *Pseudoacanthocephalus goodmani* can be placed between *P. perthensis* (Edmonds, 1971) and *P. reesei* (Bush et al., 2009), species that have 12–15 longitudinal rows of 4–5 hooks, and *P. lutzi* (Hamman, 1891), *P. bufonis* (Shipley, 1903) and *P. bufonicola* (Kostylew, 1941), species with 16–19 longitudinal rows of 5–8 hooks (Tkach et al., 2013).

*Pseudoacanthocephalus goodmani* can be further distinguished from *P. perthensis* in being a larger worm (males 4–11 mm compared with 2.6–3.2 mm long) with a cylindrical, not subcylindrical to ovoid proboscis, having the lemnisci longer than the proboscis receptacle, not about the same length and larger eggs (72.6–85.8 long compared with 45–55) (Edmonds, 1971). *Pseudoacanthocephalus reesei* in amphibians from China and usually with rows of four hooks can be further distinguished from *P. goodmani* in having the proboscis hooks increase progressively in length from anterior to posterior, the posteriormost hook being considerably larger compared with hooks 1 and 5 being smaller than hooks 2–4, the largest hooks being up to 131 in length compared with 109, and having larger eggs, 84–96 long compared with 73–86 for *P. goodmani* (see Bush *et al.*, 2009).

As redescribed by Arredondo & Gil de Pertierra (2009) and Amin & Heckmann (2014), *P. lutzi*, a South American species, has a proboscis hook formula of 14–18, usually 15–16, longitudinal rows of 5–8 proboscis hooks, which is similar to that of *P. goodmani* with 14–18, but usually 14, longitudinal rows of no more than 4–6 hooks. The hooks of *P. lutzi* are longer, up to 115 in males, 118 in females, progressively increasing in length posteriorly and with spatulate roots, compared with hook lengths of up to 99 in males and 106 in females, hooks 1 and 5/6 usually smaller and with simple roots for *P. goodmani*. Males of *P. lutzi* have testes in the posterior third of the trunk, pyriform cement glands, a sigmoid-shaped posterior end compared with those of *P. goodmani*, which have equatorial testes, elongated cement glands and the posterior end of the male not sigmoid in shape (comparative measurements are given in table 1).

*Pseudoacanthocephalus bufonis* from South-East Asia and Southern China as per Bush *et al.* (2009) has a shorter proboscis (408–542) of usually 16 alternating rows of 5–6 hooks each, the hooks measuring up to 104 long and about the same length from anterior to posterior along the proboscis. The proboscis of *P. goodmani* is longer (302–629) and the hooks, up to 109 long, vary in length from anterior to posterior, with hooks 2–4 longer than hooks 1 and 5/6 (Bush *et al.*, 2009). Trunk length of *P. bufonicola*, from Central Asia and Eastern Europe, does not exceed 10 mm and the proboscis armature, with the posterior two hooks in each row rootless and hooks 4, 5 longest, distinguishes the species from *P. goodmani*, which is up to 19 mm long and has a proboscis armature with all hooks having roots and hooks 2–4 longest (Petrochenko, 1958; Golvan, 1969).

Although having a similar proboscis hook formula to *Pseudoacanthocephalus nguyenthileae* (Amin *et al.*, 2008), *P. goodmani* differs in having 14–18 longitudinal rows of 4–6 hooks, usually 14 rows of five hooks, hooks 1 and 5/6 usually smallest, and six cement glands compared with 16–18 (rarely 15

able 1. Comparative measureme	nts of <i>Pseudoacanthocep</i>	halus goodmani and	P. lutzi. Data from Arred	ondo & Gil de Pertie	erra (2009) and Amin & Hec	:kmann (2014).		
			Pseudoacanthoce	phalus lutzi			Pseudoacanthocephc	lus goodmani
	Peru		Brazil, type m	naterial	Argentina		Mauritiu	S
	Male	Female	Male	Female	Male	Female	Male	Female
Trunk length (mm)	6.8-7.75	11.8-16.5	8.2-12	14–20	4–8.8	7-21	6-11	14-19
Proboscis length	437-603	510-676	670	740-840	350–560	400-640	302-629	502-605
Longest hooks	06	100	118	115	06	115	102	109
Neck length	I	Ι	120	320	120-220	100-340	147–235	170-368
Proboscis receptacle length	830-1190	510-676	700-860	770-1000	550-1000	710-1560	737-850	782-1122
Lemnisci	770-1180	1150-1350	480-960	670–970	650-1260	380-1780	703-1166	1105-1608
Testis anterior	$624-800 \times 458-800$		580-830 × 390-690		$460-1300 \times 260-710$		503-603 × 355-408	
Testis posterior	$572-875 \times 406-775$		650-830 × 380-650		$440-1100 \times 260-670$		516-629 × 295-482	
Cement gland length	400-575		380-650		225-850		900-1900	
Female reproductive system		1230		1300-1600		700-1600		935-1870
Eggs		70-77 × 22-27		82-93 × 29-42		54-88 × 19-39		73-86 × 23-26

or 19) rows of 5–6 hooks, hooks longest posteriorly and eight cement glands (Amin *et al.*, 2008).

*Pseudoacanthocephalus coniformis* (Amin *et al.*, 2014), described more recently than could be included in the key of Tkach *et al.* (2013), differs from *P. goodmani* in having a cone-shaped anterior trunk, a proboscis hook formula of 13 rows of seven hooks, up to 75 long, sub-equal lemnisci and eight cement glands (Amin *et al.*, 2014).

Most of the species of the genus *Pseudoacanthocephalus* are from Asian or associated regions (Amin *et al.*, 2014). Two species are known from Madagascar, one from Tanzania and *P. goodmani* from Mauritius, with a probable origin in South Africa (see the following section), which is the fourth of the 19 accepted species to be found in the African region.

# Discussion

Adult acanthocephalans being expelled in host faeces appears to be an unusual event. It is not referred to by Kennedy (2006) in his discussion of acanthocephalan life cycles and their transmission. The only record we could find of such an event happening was from Kidov *et al.* (2018), who reported finding adults of *Acanthocephalus falcatus* (Froelich, 1789), *A. ranae* (Shrank, 1788), *P. bufonis* and *Pseudoacanthocephalus caucasicus* (Petrochenko, 1953) in the Caucasian toad *Bufo verucossismus* (Pallas, 1814). Perhaps the phenomenon is more common in toads than the literature would suggest but has previously gone unnoticed.

As indicated above, *P. lutzi* and *P. goodmani* are morphologically similar and the cane toad, *Rhinella marina* (Linnaeus, 1758), the type host of *P. lutzi* (see Arredondo & Gil de Pertierra, 2009), was introduced into Mauritius between 1936 and 1938 (Cheke & Hume, 2008). *Pseudoacanthocephalus lutzi* has been reported from a range of amphibian hosts across South America and the West Indies (Arredondo & Gil de Pertierra, 2009; Amin & Heckmann, 2014, Drake *et al.*, 2014; Toledo *et al.*, 2017) but not from any of the other countries where *R. marina* has been introduced. Barton (1997) reported that only local parasites had been recorded from Australian cane toads and Barton & Pichelin (1999) recorded only *P. bufonis* from cane toads in Hawaii, thereby supporting the finding that the species *P. goodmani* is distinct from *P. lutzi*.

As Mauritius possesses no native species of amphibians, either *P. goodmani* was introduced from South Africa with its host *S. gutturalis* or *P. goodmani* arrived in Mauritius with the introduction of the cane toad, *R. marina*, and subsequently infected *S. gutturalis*. Given that *P. lutzi* has been reported only from American hosts, this latter scenario seems most unlikely.

The problem of the effects of non-native, sometimes invasive species in contributing to the current global biodiversity crisis is increasingly recognized (e.g. Jardine & Sanchirico, 2018; Bélouard *et al.*, 2019). For example, the American bullfrog, *Lithobates catesbianus* Shaw 1802, has been deliberately or inadvertently released on several continents and in many countries (including the UK) and frequently persists extremely well, acting as an invasive predator, competitor and vector of diseases (Cunningham, 2018; Urbina *et al.*, 2018). Introduced species of current concern in the UK include the marsh frog, *Pelophylax ridibundus* (Pallas, 1771), and its congeners, and the alpine newt, *Ichthyosaura alpestris* (Laurenti, 1768), both of which are associated with the detection of the fungal pathogen, *Batrachochytrium dendrobatidis* (Bd), in the wild (Smith, 2013).

While it is unlikely that S. gutturalis could easily become established in the wild in northern Europe, the species' adaptability and latitudinal and altitudinal range make this impossible to rule out. Further, accidental stowaways of the species to the UK are likely to be very infrequent. More pertinent is perhaps the concern that stowaway non-native amphibians could introduce novel pathogens and, particularly, novel parasites with unknown environmental tolerances such as P. goodmani, if or when released into the wild. Despite having an indirect life cycle, acanthocephalans have been known to invade and extend their range by travelling with introduced or invading hosts. For example, Plagiorhynchus cylindraceus, a common parasite of passerine birds as definitive hosts and mammals as paratenic hosts, originating in Europe, is known to have invaded Australia and North America using introduced and then indigenous birds as hosts (Moore, 1983; Smales, 2002). Similarly, P. cylindraceus has invaded New Zealand, probably with isopod intermediate hosts, and has been detected in hedgehogs, alien pests in this context, as paratenic hosts (Skuballa et al., 2010). The introduction of Acanthogyrus (Acanthosentis) alternatespinus Amin, 2005 in Lake Biwa, Japan, has been similarly attributed to the introduction of its host Rhodeus ocellatus ocellatus (Kner, 1866) from eastern China and the Korean Peninsula (Amin, 2005). Fortunately, in the present situation, the unwitting couriers of the toad in question were responsible enough not to release it into the surrounding countryside. This example of the unplanned arrival of toad plus acanthocephalan parasite into the UK, however, illustrates the need for vigilance in controlling the entry of potentially invasive species.

The toad has been maintained in isolation in captivity by J.W.W. since early 2016 and remains apparently healthy, although it has not been tested for Bd or other pathogens. The husbandry routine is such that other captive specimens are not brought into contact with any of the terrarium contents. The appetite and activity patterns of the toad appear to be normal, and no more parasitic worms have been recovered, despite regular checking.

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#### Conflicts of interest. None.

**Ethical standards.** The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals.

## References

- Amin OM (2005) Occurrence of the subgenus *Acanthosentis* Verma & Datta, 1929 (Acanthocephala: Quadrigyridae) in Japan with the description of *Acanthogyrus (Acanthosentis) altenatspinus* n. sp. and *A. (A.) parareceptaclis* n. sp. from Lake Biwa drainage fishes and a key to the species of the subgenus. *Systematic Parasitology* **60**, 125–127.
- Amin OM and Heckmann RA (2014) First description of Pseudoacanthocephalus lutzi from Peru using SEM. Scientia Parasitologica 15, 19–26.
- Amin OM, Van Ha N and Heckmann RA (2008) New and already known acanthocephalans from amphibians and reptiles in Vietnam, with keys to species of *Pseudoacanthocepalus* Petrochenko, 1956 (Echinorhynchidae)

and Sphaerechinorhynchus Johnston and Deland, 1929 (Plagiorhynchidae). Journal of Parasitology **94**, 181–189.

- Amin OM, Heckmann RA and Van Ha N (2014) Acanthocephalans from fishes and amphibians in Vietnam, with descriptions of five new species. *Parasite* 21, 53.
- Arredondo NJ and Gil de Pertierra AA (2009) Pseudoacanthocephalus lutzi (Hamann, 1891) comb n. (Acanthocephala: Echinorhynchidae) for Acanthocephalus lutzi Hamman, 1891), a parasite of South American amphibians. Folia Parasitologica 56, 295–304.
- Barton DP (1997) Introduced animals and their parasites: the cane toad Bufo marinus, in Australia. Australian Journal of Ecology 22, 316-324.
- Barton DP and Pichelin S (1999) Acanthocephalus bufonis (Acanthocephala) from Bufo marinus (Bufonidae: Amphibia) in Hawaii. Parasite 6, 269–272.
- Bélouard N, Petit EJ and Paillisson JM (2019) Variable effects of an invasive species on the reproduction and distribution of native species in pond networks. *Freshwater Biology* 64, 544–554.
- Bush SE, Duszynski DW and Nickol BB (2009) Acanthocephala from amphibians in China with the description of a new species of *Pseudoacanthocephalus* (Echinorhynchida). *Journal of Parasitology* 95, 1440–1445.
- Channing A (2001) Amphibians of Central and Southern Africa. 470 pp. Ithaca and London, Cornell University Press.
- Cheke A and Hume JP (2008) Lost land of the Dodo: an ecological history of Mauritius, Réunion and Rodrigues. 464 pp. London, T. and A.D. Poyser.
- Cunningham AA (2018) Infectious disease threats to amphibian conservation. Glasgow Natural History Society (Supplement) 27, 81–90.
- Drake MC, Zeiger U, Growskowski A, et al. (2014) Survey of helminths, ectoparasites, and chytrid fungus of an introduced population of cane toads, *Rhinella marina* (Anura: Bufonidae), from Grenada, West Indies. Journal of Parasitology 100, 608–615.
- Edmonds SJ (1971) Australian Acanthocephala no. 13: three new species. Transactions of the Royal Society of South Australia 95, 55–60.
- Golvan YJ (1969) Systematique des acanthocephales (Acanthocephala Rudolphi 1801). Premiere partie: l'ordre des Palaeacanthocephala Meyer 1931, premier fascicule: la super-famille des Echinorhynchoidea (Cobbold 1876) Golvan et Houin 1963. Mémoires du Muséum National D'Histoire Naturelle Série A 57, 1–373.
- IUCN SSC Amphibian Specialist Group (2016) Sclerophrys gutturalis. The IUCN Red List of Threatened Species 2016: e.T54659A107346817. Available at http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T54659A107346817.en (accessed 26 September 2019).
- Jardine SL and Sanchirico JN (2018) Estimating the cost of invasive species control. *Journal of Environmental Economics and Management* 87, 242–257.
- Kennedy MJ (1982) A redescription of Acanthocephalus bufonis (Shipley, 1903) Southwell and Macfie, 1925 (Acanthocephala: Echinorhynchidae)

from the black-spotted toad, *Bufo melanostictus*, from Bogor, Indonesia. *Canadian Journal of Parasitology* **60**, 356–360.

- Kennedy RC (2006) *Ecology of the Acanthocephala*. 249 pp. Cambridge, UK, Cambridge University Press.
- Kidov AA, Kondakova V, Matushinka KA and Afrin KA (2018) Notes on the helminthofauna of the Caucasian toad, *Bufo verrucosissmus* (Pallas, 1814). *Rossiiskii Parazitologicheskii Zhurnal* 4, 16–23 (in Russian).
- Moore J (1983) Responses of an avian predator and its isopod prey to an acanthocephalan parasite. *Ecology* 64, 1000-1015.
- Petrochenko VI (1956) Acanthocephala of domestic and wild animals. Vol I. 465 pp. Moscow, Istadel'stovo Akademii Nauk SSSR (in Russian: English translation by Israel Program for Scientific Translations, Jerusalem, 1971).
- Petrochenko VI (1958) Acanthocephala of domestic and wild animals. Vol II. 478 pp. Moscow, Istadel'stovo Akademii Nauk SSSR (in Russian: English translation by Israel program for Scientific Translations, Jerusalem, 1971).
- Skuballa J, Taraschewski H, Petney TN, Pfaffle M and Smales LR (2010) The avian acanthocephalan *Plagiorhynchus cylindraceus* (Palaeacanthocephala) parasitizing the European hedgehog (*Erinaceus europaeus*) in Europe and New Zealand. *Parasitology Research* 106, 431–437.
- Smales LR (2002) Plagiorhynchidae Meyer, 1931 (Aanthocephala) from Australasian birds and mammals, with descriptions of *Plagiorhynchus* (*Plagiorhynchus*) menurae (Johnston, 1912) and *P. (P.) allisonae* n. sp. Systematic Parasitology 51, 207–216.
- Smith F (2013) *The epidemiology of the amphibian pathogen* Batrachochytrium dendrobatidis *in the UK.* 193 pp. PhD Thesis, Imperial College London.
- Spawls S, Howell K and Drewes RC (2006) Reptiles and Amphibians of East Africa: a Princeton Pocket Guide. 240 pp. Princeton, USA, Princeton University Press.
- Telford NS, Channing A and Measey J (2019) Origin of invasive populations of the Guttural Toad (*Sclerophrys gutturalis*) on Reunion and Mauritius Islands and in Constantia, South Africa. *Herpetological Conservation and Biology* 14, 380–392.
- Tkach VV, Lisitsyna OI, Crossley JL, Binh TT and Bush SE (2013) Morphological and molecular differentiation of two species of *Pseudoacanthocephalus* Petrochenko, 1958 (Acanthocephala: Echinorhynchidae) from amphibians and reptiles in the Philippines, with identification key for the genus. *Systematic Parasitology* **85**, 11–26.
- Toledo G, de Fonesca MG, Iannacone J, Cardenas Callirgos JM, Pineda Castilla C and da Silva RJ (2017) Infection with Pseudoacanthocephalus lutzi (Hamman, 1891) (Acanthocephala: Echinorhynchidae) in Rhinella marina (Linneaus, 1785) (Amphibia: Bufonidae) in Peru. Neotropical Helminthology 11, 405–411.
- Urbina J, Bredeweg EM, Garcia TS and Blaustein AR (2018) Host-pathogen dynamics among the invasive American bullfrog (*Lithobates catesbeianus*) and chytrid fungus (*Batrachochytrium dendrobatidis*). Hydrobiologia 817, 267–277.