

## Occurrence of acanthocephalans in the Eurasian otter *Lutra lutra* (L.) (Carnivora, Mustelidae) in Bulgaria, with a survey of acanthocephalans recorded from this host species

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### Summary

Three Eurasian otters (*Lutra lutra*) originating from Pazardzhik Region (South Bulgaria) were examined for helminth parasites. Three species of acanthocephalans were recorded: *Pomphorhynchus laevis*, *Acanthocephalus anguillae* and *A. ranae*. These species are not specific parasites of otters, the former two occurring in various freshwater fishes and the latter being a parasite of anurans. A review of acanthocephalan species recorded from *L. lutra* is presented. The possible transmission routes by which otters become infested with acanthocephalans are considered to be either paratenic transfer of encysted extra-intestinal juveniles in paratenic hosts or postcyclic transmission of mature intestinal worms in definitive hosts.

Key words: Acanthocephala, Eurasian otter, Bulgaria

### Introduction

According to the international criteria, the Eurasian otter *Lutra lutra* (L.) is classified as a near threatened species (IUCN, 2007). It is also of great conservational importance in Bulgaria (Popov and Sedefchev, 2003). Mostly for this reason, its helminth fauna is poorly studied. The only helminth species recorded from this host in Bulgaria is the digenetic *Euryhelmis squamula* (Rudolphi, 1819) (see Janchev, 1987). No acanthocephalans were previously reported from Eurasian otters in this country. The aim of this article is to report on the acanthocephalans recorded in Eurasian otters from Bulgaria and to present a survey on acanthocephalans recorded from this host species throughout its geographical range.

### Materials and Methods

The present study was based on acanthocephalans isolated

from three road-killed Eurasian otters originating from the vicinities of the village of Yunatsite (Pazardzhik Region) in the period 1996 – 1999. The data about the collection date and the number of specimens are presented in the section for each species. The specimens were fixed and preserved in 70 % ethanol. They were cleared in glycerol (25 – 100 %) or dimethylphthalate and studied in temporary mounts. The measurements are in millimetres unless otherwise stated. Figures given in parentheses after the range are those of single measurements outside the normal range.

### Results

Three species of acanthocephalans were found in the course of the present study:

Class Palaeacanthocephala Meyer, 1931

Order Echinorhynchida Southwell & MacFie, 1925

Family Echinorhynchidae Cobbold, 1876

*Acanthocephalus anguillae* (Müller, 1780) Lühe, 1911  
(Fig. 1. A – D)

Specimens studied: 3 females, February 1999.

Description (based on 3 females):

Trunk elongate, almost cylindrical, narrowing posteriorly; 7.60 – 9.52 long and 0.93 – 1.24 wide. Proboscis elongate-oval, situated at angle to trunk axis; 0.73 – 0.76 long and 0.28 – 0.34 wide. Proboscis armament consists of 8 – 10 longitudinal rows of 5 (6) hooks in each row. Hooks with well developed roots, posteriorly directed. Roots with two antero-lateral processes; only roots of some last hooks without such processes. Length of first 4 (5) hooks - blade 81 – 188 (194) µm, root 53 – 97 µm, anterior processes 13 – 25 (30) µm; Length of last hook - blade 33 – 78 µm, root 30 – 55 µm. Neck almost cylindrical, 0.60 – 0.70 long and 0.28 – 0.31 wide. ‘Pseudocollum’ trapezoid, 0.26 – 0.37

long and 30 – 38 wide (at anterior end) and 0.43 – 0.52 wide (at posterior end). Proboscis receptacle cylindrical, double-walled, attached at proboscis base; 0.95 – 0.97 long and 0.17 – 0.24 wide. Lemnisci enlarged and rounded at posterior end, 0.83 – 1.00 long and 0.13 – 0.26 wide. Female genital tract about 0.70 – 1.30 long. Vagina provided with one sphincter. Genital pore terminal. Numerous unripe eggs observed through body wall, 54 – 61  $\mu\text{m}$  long and 37 – 44  $\mu\text{m}$  wide, without polar prolongations.

#### Remarks:

Comparing morphometric data of the present specimens with previous descriptions (Lühe, 1911; Petrochenko, 1956; Čanković *et al.*, 1968; Rokicki, 1970; Andryuk, 1979; Kakacheva-Avramova, 1983; Brown *et al.*, 1986), we found some differences. The longitudinal rows of hooks in our material range from 8 to 10, while according to the mentioned above authors, the number of longitudinal rows is ten. The maximum dimensions of the hooks of the present specimens are most similar to specimens from Poland, 198  $\mu\text{m}$  (Rokicki, 1970) vs 194  $\mu\text{m}$  in Bulgarian material. Petrochenko (1956) and Lühe (1911) recorded smaller dimensions of hooks, 136  $\mu\text{m}$  and 140  $\mu\text{m}$  (the latter taken from the drawing), respectively. The description by Kakacheva-Avramova (1983) was based mostly on male specimens and dimensions of the hooks of female specimens are presented as ‘greater than those of the male specimens’ (i.e., more than 97  $\mu\text{m}$ ).

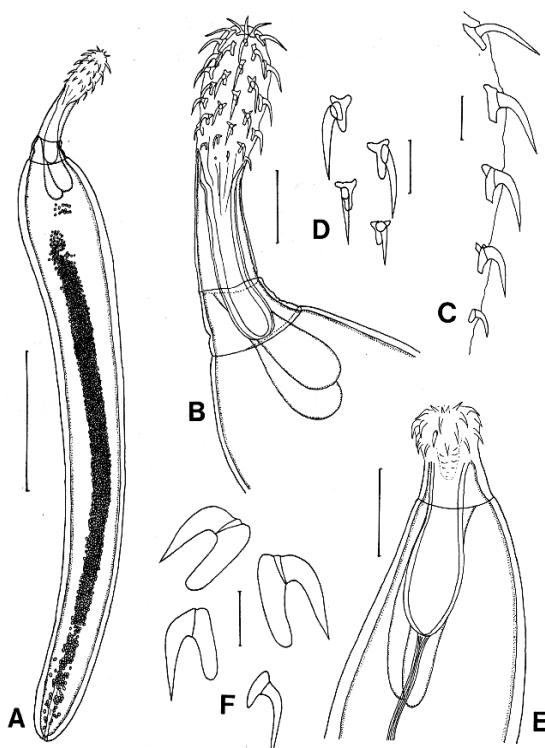


Fig. 1. *Acanthocephalus* spp. A – D: *A. anguillae* (Müller, 1780), Females: A - General view; B - Proboscis and anterior part of trunk; C - Longitudinal row of hooks (lateral view); D - Hooks, frontal view. E – F: *A. ranae* (Schrank, 1788), Female: E - Proboscis and anterior part of trunk; F - Last two hooks in two adjacent rows (lateral view). Scale-bars = 2.0 mm (A); 0.4 mm (B, E); 0.1 mm (C, D); 0.05 mm (F)

The specimens studied possess a ‘pseudocollum’ posteriorly to the neck (Figure 1 A, B). Achmerov and Dombrowskaja-Achmerova (1941) erected the genus *Paracanthocephalus* for species with a pseudocollum. Some authors (Yamaguti, 1963; Amin, 1985, Golvan, 1994) considered this genus as a synonym of *Acanthocephalus* Koelreuter, 1771. Kakacheva-Avramova (1983) recorded *Paracanthocephalus tenuirostris* Achmerov & Dombrowskaja-Achmerova, 1941 from Bulgaria. The proboscis armament of the Bulgarian materials consists of 6 or 7 – 8 longitudinal rows, 5 or 5 – 6 hooks in row, with maximum length of hooks 98 – 117  $\mu\text{m}$  and length of eggs are 83 – 117  $\mu\text{m}$  (Kakacheva-Avramova, 1983) vs 6 longitudinal rows, 5 hooks in row, maximum length of hooks 119  $\mu\text{m}$  and length of eggs 40 – 41  $\mu\text{m}$  in materials from the Russian Far East (Achmerov and Dombrowskaja-Achmerova, 1941; Achmerov, 1959). Furthermore, the material of Kakacheva-Avramova (1983) corresponds to some characters of *Paracanthocephalus rauschi* Schmidt, 1969 from Alaska (6 – 8 longitudinal rows, 5 – 6 hooks in row, maximum length of hooks – 130 – 167  $\mu\text{m}$  and length of eggs are 65 – 88  $\mu\text{m}$ ) (Schmidt, 1969). The present female specimens possess a pseudocollum but strongly resemble *A. anguillae* in the remaining characters, thus supporting the synonymy of the genera *Acanthocephalus* and *Paracanthocephalus*. *A. anguillae* has been recorded from *Salmo trutta fario* L., *Esox lucius* L., *Leuciscus cephalus* (L.), *L. idus* (L.), *Blicca bjoerkna* (L.), *Rutilus rutilus* (L.), *Alburnus alburnus* (L.), *Barbus meridionalis* Risso and *B. cyclolepis* Heckel (= *B. tauricus cyclolepis* Heckel) in Bulgaria (Kakacheva-Avramova, 1983; Kirin, 2000; 2001a; 2001b; 2002a; 2002b; 2002c; 2003c; Kirin *et al.*, 2003; 2005). The occurrence of *A. anguillae* in the Eurasian otter is a new host record in Bulgaria. Previously, *A. anguillae* was reported from *L. lutra* in Sweden (Lundström, 1942), Germany (former DDR) and Austria (Reitter, 2001) (Table 1).

#### *Acanthocephalus ranae* (Schrank, 1788) Lühe, 1911 (Fig. 1. E-F)

Specimens studied: 1 female, April 1996.

#### Description – female:

Trunk elongate, cylindrical, narrowing posteriorly; 13.40 long and 0.92 wide. Numerous fragments of hypodermal nuclei observed. Proboscis about 0.50 long (partly invaginated) and 0.28 wide. Proboscis armament consists of 16 longitudinal rows, 2 hooks in each row (the anterior 3 – 4 hooks invaginated and are probably 4th – 5th or 5th – 6th hooks. Hooks with well-developed roots, posteriorly directed. In every second row, last hook is smaller, with shorter root. Length of anterior hooks: blade 78 – 88  $\mu\text{m}$ , root 64 – 83  $\mu\text{m}$ . Length of posterior hooks: blade 83 – 86  $\mu\text{m}$  and root 62 – 66  $\mu\text{m}$ , or blade 52 – 64  $\mu\text{m}$  and root 29 – 39  $\mu\text{m}$ . Neck trapezoid, 0.23 long, 0.26 wide (at anterior end) and 0.35 wide (at posterior end). Proboscis receptacle sacciform, double-walled, attached at proboscis base; 0.86 long and 0.26 wide. Lemnisci 1.00 long and 0.15 wide. Female genital tract about 1.20 long. Vagina provided with one sphincter. Genital pore terminal. Numerous unripe

eggs (without polar prolongations) observed through body wall, 56 – 81  $\mu\text{m}$  long and 29 – 39 (66)  $\mu\text{m}$  wide.

#### Remarks:

Comparing morphometric data of the present specimen with previous descriptions (Lühe, 1911; Petrochenko, 1956; Grabda-Kazubska, 1962; Golvan, 1969), we find a greater maximum length of hooks (86 – 88  $\mu\text{m}$ ) in comparison with the data (70 – 71  $\mu\text{m}$ ) of Lühe (1911), Petrochenko (1956) and Golvan (1969). In relation to this character, our material is more similar to the specimens from Poland and Bulgaria - 91 – 95  $\mu\text{m}$  and 80 – 85  $\mu\text{m}$ , respectively (Grabda-Kazubska, 1962; Dimitrova, 1998).

Previously, this species was recorded from *Bombina variegata* (L.), *Bufo viridis* Laurenti, *Hyla arborea* (L.), *Rana ridibunda* Pallas, *R. esculenta* L., *R. temporaria* L., *R. dalmatina* Fitzinger in Bonaparte and *R. graeca* Boulenger in Bulgaria (Bachvarov, 1977; 1982a; 1982b; 1983; 1984; Bachvarov and Petrov, 1978; Kirin, 2003a; 2003b). Dimitrova *et al.* (2000) recorded this species from *Larus argentatus* Pontoppidan in Bulgaria. The finding of *A. ranae* in the otter is a new host record for Bulgaria. The other record of *A. ranae* in *L. lutra* is from Romania (Chiriac and Barbu, 1968, see Table 1).

#### Family Pomphorhynchidae Yamaguti, 1939

*Pomphorhynchus laevis* (Zoega in Müller, 1776) Van Cleave, 1924 (Fig. 2)

Specimens studied: 1 male, 1 female and 1 metasoma - juveniles, February 1999; 1 adult female, March 1999.

Description (based on 2 juvenile specimens), February 1999:

Male. Trunk 2.22 long and 0.93 wide. Proboscis cylindrical, 0.53 long (0.34 evaginated and 0.19 invaginated), 0.23 wide at base. Proboscis armament consists of 17 longitudinal rows, 6 – 7 hooks in each row (anterior 3 – 4 hooks invaginated). Hooks with well-developed roots, posteriorly directed. Length of hooks: blade 35 – 50  $\mu\text{m}$ , root 22 – 49  $\mu\text{m}$ . Neck cylindrical, 1.40 long and 0.40 wide; anterior part of neck transformed into bulb, 0.40 long and 0.36 wide. Proboscis receptacle double-walled, attached at proboscis base, 1.23 long and 0.11 wide. Lemnisci cannot be measured. Testes oval, situated in tandem, 0.23 – 0.28 long and 0.15 – 0.18 wide. Cement glands and ducts not distinct.

Female. Trunk 3.00 long and 1.30 wide. Proboscis cylindrical, 0.62 long and 0.20 wide. Proboscis armament consists of 17 longitudinal rows, 10 – 11 hooks in each row. First 8 hooks with well-developed roots, posteriorly directed. Roots of next two hooks also directed posteriorly, but possess small apophyses (5 – 7  $\mu\text{m}$  long); most posterior hooks with root directed anteriorly. Length of first 5 hooks: blade 47 – 54  $\mu\text{m}$ , root 40 – 59  $\mu\text{m}$ ; length of next 5 hooks: blade 40 – 48  $\mu\text{m}$ , root 27 – 47  $\mu\text{m}$ ; length of last hooks: blade 37  $\mu\text{m}$ , root 27  $\mu\text{m}$ . Neck cylindrical, 1.80 long and 0.44 wide; anterior part of neck transformed into bulb, 0.80 long and 0.65 wide. Proboscis receptacle double-walled, attached at proboscis base, 1.32 long and

0.19 wide. Lemnisci deformed, about 1.0 long. Vagina provided with one sphincter. Genital pore terminal.

Additional data (based on one adult female, March 1999): Trunk 9.3 long and 1.9 wide. Proboscis about 0.50 long (the remaining part invaginated in a bulb). Proboscis armament consists of 18 longitudinal rows, 7 – 8 hooks in row (remaining hooks invaginated in a bulb). Length of anterior 3 – 4 hooks: blade 50 – 53  $\mu\text{m}$ , root cannot be measured. Neck 2.40 long and 0.68 wide; anterior part of neck and bulb deformed. Female genital tract about 2.40

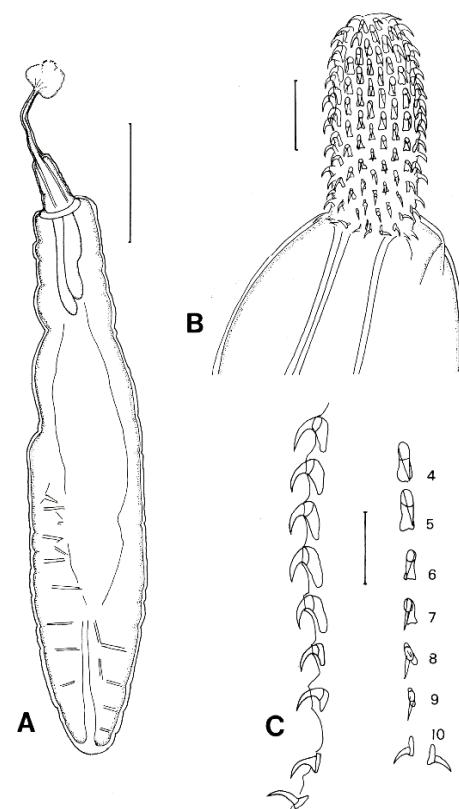


Fig. 2. *Pomphorhynchus laevis* (Zoega in Müller, 1776), Females: A – General view of adult specimen; B – Proboscis and part of bulb of juvenile specimen; C – Longitudinal rows of hooks (left – lateral view, right – frontal view). Scale – bars = 2.0 mm (A); 0.2 mm (B); 0.1 mm (C)

long. Numerous ovarian balls seen through body wall.

#### Remarks:

The present specimens have a shorter proboscis, 0.53 – 0.62 mm versus 0.70 – 0.90 mm (Kostylev, 1928, cited after Petrochenko, 1956; Meyer, 1933; Petrochenko, 1956; Čanković *et al.*, 1968; Brown *et al.*, 1986) and are comparable with the minimum dimensions of the proboscis presented by Lühe (1911), i.e. 0.60 – 1.00, and Kakacheva-Avramova (1983), i.e. 0.49 – 1.50. Another difference concerns the armature of the proboscis, i.e. 17 – 18 longitudinal rows, 10 – 11 hooks in each row in specimens studied vs 18 – 21, 11–13 hooks per row (Lühe, 1911; Kostylev, 1928, cited after Petrochenko, 1956; Meyer, 1933; Petrochenko, 1956; Čanković *et al.*, 1968; Kakacheva-Avra-

mova, 1983). On the basis of this character, our specimens are comparable to those from Great Britain having 13–20 longitudinal rows, 8–13 hooks in each row (Brown *et al.*, 1986). In addition, the maximum dimensions of the hook blades are greater (47–54; 40–48; 37 µm, respectively), since previous authors (Kostylev, 1928, cited after Petrochenko, 1956; Petrochenko, 1956; Čanković *et al.*, 1968) reported 48–50, 33–40 and 19–20 µm, respectively, for this character. Kakacheva-Avramova (1983) only reported longer blades of the last hooks (48 µm).

In Bulgaria, *P. laevis* was recorded from about 50 freshwater fish species (Kakacheva-Avramova, 1983; Kirin, 2000; 2001b; 2006; Kirin *et al.*, 2005). In 12 of these hosts (mainly of the family Gobiidae), the acanthocephalans were found as encysted juveniles in the intestinal wall, body cavity, liver and gall-bladder (Margaritov, 1966; Kakacheva-Avramova, 1972, 1973, 1977). Encysted juveniles of this species were also found in *Rana ridibunda* (wall of the small intestines, gall-bladder) from North Bulgaria (Bachvarov *et al.* 1976). The finding of *P. laevis* in the otter is a new host record in Bulgaria. Reitter (2001) recorded this species from *L. lutra* in Germany and Austria (Table 1).

(2) infestation with encysted juveniles by eating paratenic hosts (paratenic transmission), and (3) infestation with adult parasites by eating definitive hosts (postcyclic transmission). The diet of the otter consists of fish, frogs, crabs, insects, aquatic birds and some rodents (Fairley, 1972; Fairley and Wilson, 1972; Machida, 1973; Görner and Hachethal, 1987; Macdonald and Barrett, 1993; Popov and Sedefchev, 2003; Georgiev, 2006). The acanthocephalans recorded from Eurasian otters (Table 1) have as intermediate hosts amphipods, isopods and terrestrial insects. Therefore, the infection route involving cystacanths from intermediate hosts seems less possible.

*Corynosoma strumosum* occurs in the intestine of seals, sometimes in mustelid mammals and aquatic birds; its intermediate hosts are amphipods (Petrochenko, 1958; Khokhlova, 1986). As paratenic hosts, numerous marine and freshwater fishes are known (Petrochenko, 1958; Schmidt, 1985). Infrequently, grass snakes (Sharpilo, 1976; Khokhlova, 1986), insectivores and mustelids (Prokopić and Genov, 1974; Shimalov and Shimalov, 2001) were reported as its paratenic hosts. *C. strumosum* was found in Eurasian otters in coastal habitats of British Islands (Jefferies *et al.*, 1990; Weber, 1991; McCarthy and

Table 1. Acanthocephalan species reported from *Lutra lutra* (L.)

Acanthocephalan species	Localities	References
Family Moniliformidae Van Cleave, 1924		
<i>Moniliformis moniliformis</i> (Bremser, 1811)	Caucasus	Butzeck (1984, cited after Torres <i>et al.</i> , 2004)
<i>Moniliformis</i> sp. (= <i>Gigantorhynchus</i> sp.)	Spain	Torres <i>et al.</i> (2004)
Family Arhythmacanthidae Yamaguti, 1935		
<i>Heterosentis plotosi</i> Yamaguti, 1935	Japan	Machida (1973)
Family Echinorhynchidae Cobbold, 1876		
<i>Acanthocephalus anguillae</i> (Müller, 1780)	Sweden	Lundström (1942)
	Germany and Austria	Reitter (2001)
<i>A. lucii</i> (Müller, 1776)	Sweden	Lundström (1942)
	Germany and Austria	Reitter (2001)
<i>Acanthocephalus</i> sp. (= <i>A. cf. ranae</i> Schrank, 1788)	Romania	Chiriac and Barbu (1968)
<i>Acanthocephalus</i> sp.	Ireland	Fairley (1972)
<i>Acanthocephalus</i> sp.	Russia (Sakhalin)	Ben'kovskiy <i>et al.</i> (1973)
<i>Acanthocephalus</i> sp.	Germany and Austria	Reitter (2001)
<i>Echinorhynchus</i> sp.	Britain (coastal sites)	Jefferies <i>et al.</i> (1990)
<i>Pseudoacanthocephalus</i> sp.	Latvia	Vismanis and Ozolins (1998)
Family Pomphorhynchidae Yamaguti, 1939		
<i>Pomphorhynchus laevis</i> (Zoega in Müller, 1776)	Germany and Austria	Reitter (2001)
Family Polymorphidae Meyer, 1931		
<i>Corynosoma strumosum</i> (Rudolphi, 1802)	Britain (coastal sites)	Jefferies <i>et al.</i> (1990)
	Shetland	Weber (1991)
	Ireland	McCarthy and Hassett (1993)
<i>Polymorphus minutus</i> (Goeze, 1782)	Germany and Austria	Reitter (2001)

## Discussion

Eight acanthocephalan species were reported from *L. lutra* (Table 1) and none of them being its specific parasite. Three possible infection routes can be considered: (1) infestation with cystacanths by ingesting intermediate hosts,

Hassett, 1993) and it is likely that various fishes had a role in the transmission acting as paratenic hosts: *Gadus morhua* L. (see Jefferies *et al.*, 1990), *Zoarces viviparus* (L.) and *Cyclopterus lumpus* L. (Weber, 1991).

Another transmission route can be associated with predation on definitive hosts. Bozhkov (1969, 1982) defined as

postcyclic parasitism the transmission of mature individuals from a definitive host to another host through predation or cannibalism. The experimental postcyclic transmission of adult intestinal worms was proved for 11 acanthocephalan species (Nickol, 2003; McCormick and Nickol, 2004). Since the postcyclic transmission is frequent in acanthocephalans, it better explains the occurrence of the remaining species in Eurasian otters (Table 1).

*Moniliformis moniliformis* (= *M. dubius* Meyer, 1932) is mainly a parasite of rodents, rarely of carnivores and insectivores (Khokhlova, 1986). Its intermediate hosts are insects belonging to the Blattidae, Tenebrionidae and Scarabaeidae (Moore, 1946; Schmidt, 1985; Khokhlova, 1986). Toads are known as experimental (Moore, 1946) and lizards as natural paratenic hosts (Sharpilo, 1976). However, these paratenic hosts were considered 'traps' for the cystacanths of this species (Sharpilo, 1979; Sharpilo *et al.*, 1996). Therefore, the infection in *L. lutra* seems more likely to originate from infected rodents.

*Heterosentis plotsosi* is a parasite of the shore fish *Plotosus lineatus* (Thunberg); its intermediate and paratenic hosts are unknown (Golvan, 1969; Schmidt, 1985). Machida (1973) considered its occurrence in the intestine of *L. lutra whiteleyi* Grey as 'accidental infection' due to its prey consisting mostly of shore fishes. Essentially, this infection is to be considered a result of postcyclic transmission of adult worms.

*Acanthocephalus anguillae* is an intestinal parasite of freshwater fishes, with isopods as intermediate hosts (Schmidt, 1985). Though it can be found in extra-intestinal sites, its life cycle is not dependent on paratenic hosts (Taraschewski, 2000). Adult specimens of *A. anguillae* were found in otters in Sweden (Lundström, 1942), Germany and Austria (Reitters, 2001), probably due to postcyclic transmission.

*A. lucii* is a parasite of freshwater fishes, with isopods as intermediate hosts (Schmidt, 1985). Extra-intestinal localization of this species is not known (Taraschewski, 2000). Lundström (1942) recorded 28 adult specimens from one otter in Sweden. Reitter (2001) reported this and other acanthocephalan species from otters in Germany and Austria as 'pseudoparasites'. These two records also seem to be cases of postcyclic parasitism. Another postcyclic record of this species is its occurrence in kingfisher, *Alcedo atthis* (L.), in Bulgaria (Dimitrova *et al.*, 2000).

*A. ranae* is a parasite mainly of anurans, having isopods as intermediate hosts; paratenic hosts are not known (Schmidt, 1985). Chiriac and Barbu (1968) recorded 10 specimens in bad condition from the intestine of an otter and identified them as '*A. cf. ranae*'. Bozhkov (1980) studied experimentally the success of the postcyclic transmission of *A. ranae* from *Rana ridibunda* to *Bufo viridis*. There are several further records of adults of *A. ranae* in *Natrix natrix* (L.) in Ukraine and Belarus (Sharpilo, 1976; Shimalov and Shimalov, 2000), *Vipera berus* (L.) in Poland (Lewin and Grabda-Kazubska, 1997) and *Larus argentatus* in Bulgaria (Dimitrova *et al.*, 2000). All these cases may represent postcyclic parasitism.

*Polymorphus minutus* is a parasite of aquatic birds, with amphipod intermediate hosts; paratenic hosts are unknown (Schmidt, 1985). The record of *P. minutus* in otters (Reitter 2001) seems to be a result of postcyclic transmission. Aquatic birds were reported as prey of otters by several studies (Fairley, 1972; Görner and Hachethal, 1987; Macdonald and Barrett, 1993; Georgiev, 2006).

*P. laevis* is a widespread intestinal parasite of freshwater fishes, with amphipod intermediate hosts (Schmidt, 1985). It is also known from extra-intestinal sites (Taraschewski, 2000). Various fishes (Margaritov, 1966; Čanković *et al.*, 1968; Kakacheva-Avramova, 1972, 1973, 1977) and frogs (*Rana ridibunda*) (Bachvarov *et al.*, 1976) were recorded as paratenic hosts. However, its ability for postcyclic transmission was experimentally proved (Kennedy, 1999). Therefore, both transmission routes (paratenic and postcyclic) seem possible in relation to this species.

On the basis of data presented above, we consider the specimens of *A. anguillae* and *A. ranae* found by us in the intestine of the otters as a probable result of postcyclic transmission from their definite hosts (fishes and frogs, respectively). Therefore, *L. lutra* ought to be regarded as a postcyclic host of these acanthocephalans. In relation to *P. laevis*, both postcyclic and paratenic transmission routes seem possible.

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