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A redescription of *Protospirura muricola* Gedoelst, 1916 (Nematoda: Spiruridae), a parasite of murid rodents

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Abstract The spirurid nematode *Protospirura muricola* Gedoelst, 1916 is redescribed from *Acomys dimidiatus* (Desmarest) from the St Katherine Protectorate, Sinai, Egypt. Egyptian material closely resembled specimens of *P. muricola* from African mammals re-examined in this study, as well as conforming to published reports of this species. *P. muricola* with two denticles on each lateral lobe of the pseudolabia and six pairs of postanal papillae is closest to *P. pseudomuris* Yokohata & Abe, 1989, but can be readily distinguished in having the right spicule shorter than the left. The significance of the characteristics of the head and mouth, and of the male spicules, in characterising *Protospirura* Seurat, 1914 is evaluated. *P. muricola*, an African parasite of rodents, appears to have spread globally with synanthropic rat final hosts and possibly with the cosmopolitan dermapteran intermediate host *Leucophaea maderae* (Fabr.).

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Introduction

Protospirura Seurat, 1914 (Nematoda: Spirurida) has had a long and difficult taxonomic history, because of confusion with the similar *Mastophorus* Diesing, 1853, caused by the choice of inappropriate characters to separate these two genera (Wertheim, 1962). Although older, following the erection of *Protospirura* by Seurat (1914), *Mastophorus* was treated either as a junior synonym (e.g. Baylis & Daubney, 1926), or regarded as insufficiently known (Yorke & Maplestone, 1926). By 1926 all eight recognised species had been placed within *Protospirura* rather than within *Mastophorus* (see Yorke & Maplestone, 1926). One of these was *P. muricola* Gedoelst, 1916. Chitwood (1938) reinstated *Mastophorus*, and removed several species to it. However, *P. muricola* remained within the redefined *Protospirura*, which was reduced to four taxa; *P. numidica* Seurat, 1914, the type-species, with unequal spicules, and *P. muricola, P. bonnei* Ortlepp, 1924 and *P. suslica* Schultz, 1927, which were separated by equal or subequal spicule lengths. Read & Millemann (1953) rejected Chitwood's (1938) analysis, considering the characters used to be of subgeneric significance only. They suppressed *Protospirura* and reconstituted

Mastophorus with nine valid species and two *species inquirendae* (Read & Millemann, 1953). Yamaguti (1961) acknowledged the work of both Read & Millemann (1953) and Chitwood (1938), but returned to the older classification of Baylis & Daubney (1926), reinstating *Protospirura* with 11 valid species and suppressing *Mastophorus*. Wertheim (1962), however, may not have been aware of the classification of Yamaguti (1961) when she used that of Read & Millemann (1953) while evaluating the reliability of the characters used to differentiate the species of *Mastophorus.* She concluded that the nature of the dentition on the pseudolabia, the shape of the stoma and the form of the spicules were the most reliable characters, agreed with the suppression of *Protospirura* and reduced the number of valid species in *Mastophorus* to nine (Yamaguti, 1961; Wertheim 1962). However, studies of the morphogenesis of the larval stages of *M. muris* and *P. muricola* by Quentin (1969, 1970) validated the taxonomic decisions of Chitwood (1938) and *Protospirura* was reinstated, comprising seven valid species, including *P. muricola* with *P. bonnei* as its junior synonym.

In reviewing *Protospirura,* Hasegawa (1990) differentiated nine valid species using, amongst other characters, the number of post-anal papillae, the number of denticles on the lobes of the pseudolabia and the relative and absolute lengths of left and right spicules, noting, as described by Quentin (1969), that *P. muricola* has spicules of nearly equal length. Ten species of *Protospirura* are now recognised (Smales, 2001).

Whilst this approach has provided a useful set of characters for distinguishing the species of *Protospirura*, its validity depends on accurate descriptions of the specific characters being used. In the case of *P. muricola*, the species descriptions in the literature are often incomplete and can be confusing. For example, authors have variously described the spicules of *P. muricola* as equal or unequal in length, similar, almost similar or unequal in shape, and, in three instances, alate (Gedoelst, 1916; Ortlepp, 1924; Baylis, 1928; Brumpt, 1931; Tubangi, 1931; Foster & Johnson, 1939; Quentin, 1969; Campos & Vargas, 1978; Ashour, 1980; Scharff et al., 1993). Because *P. muricola* has been recorded from a broad range of rodents, an insectivore, a carnivore and primate hosts across Africa, Southeast Asia, the Caribbean, Central America and South America (Table 1), ensuring an accurate identification of specimens using the presently available literature may be problematical. Therefore, a comprehensive, unambiguous and accurate description of the species would be useful.

As part of a long-term study of the helminth assemblage of *Acomys dimidiatus* (Desmarest), specimens of *P. muricola* have been collected regularly from the Sinai Peninsula, Egypt. This material, either fixed for identification or cultured in laboratory mice, has been utilised to prepare the comprehensive description of *P. muricola* given below. Comparisons between the specimens of *P. muricola* from these semi-isolated sites, together with material from laboratory studies, have allowed an analysis of the variability in morphology and morphometrics between populations of worms. In this paper we compare *P. muricola* from Egyptian *A. dimidiatus* with descriptions and material from other hosts and localities in order to resolve the discrepancies in morphology noted in the published descriptions and to indicate any possible differences between worm populations. A preliminary analysis of the biogeography of this species is also given.

Materials and methods

Material was dissected from *Acomys dimidiatus* collected from the Saint Katherine Protectorate, Sinai Desert, Egypt. Hosts were collected (see Behnke et al., 2000, 2004; Bajer et al., 2006) during June, 1997, August and September, 2000, and August and September, 2004 from a variety of locations around the University of Suez Canal Environmental Research Centre (ERC) in the town of St Katherine. The local environment and general characteristics of these locations have been described in Behnke et al. (2000, 2004). *A. dimidiatus* were caught alive using Sherman traps and up to 40% of captured animals from each site were then culled (by prior agreement with Park Authorities) for the examination of endoparasites. In the majority of cases, the stomach and intestine of killed mice were dissected out and preserved in 10% formalin at ambient temperature, prior to shipping back to the UK. This material formed the basis of the present paper. Additional material was provided from a laboratory colony of this worm, established from eggs collected from St Katherine in 1997, and maintained subsequently

Table 1 Hosts and distribution of *Protospirura muricola* infections

Host		Distribution	
		Location	Region
Bathyergidae	*Heliophobius argenteocinereus* Peters	Malawi	Africa
	Cryptomys mechowi (Peters)	Zambia	Africa
	Cryptomys sp.	Zambia	Africa
Muridae	*Acomys dimidiatus* (Desmarest)	Egypt	Africa
	Arvicanthis niloticus (Desmarest)	Nigeria, Egypt	Africa
	Cricetomys emini Wroughton	Nigeria	Africa
	Cricetomys gambianus Waterhouse	D. Rep. of the Congo, Rep. of Benin	Africa
	Deomys ferrugineus Thomas	Gabon	Africa
	Gerbillus pyramidum Geoffroy	Egypt	Africa
	Grammomys rutilans (Peters)	Central African Rep.	Africa
	Heimyscus fumosus Thomas	Gabon	Africa
	Hybomys univittatus (Peters)	Central African Rep., Nigeria	Africa
	Hylomyscus stella (Brosset, Dubost & Heim de Balsac)	Gabon	Africa
	Lemniscomys striatus Linneaus	Nigeria	Africa
	Malacomys edwardsi Rochbrune	Nigeria	Africa
	Mastomys coucha (Smith)	D. Rep. of the Congo	Africa
	Mastomys erythroleucus (Temmick)	Central African Rep.	Africa
	Mus musculoides Temmink	Nigeria	Africa
	Mus musculus (Linnaeus)	Egypt, Nigeria	Africa
	Mus rufinus (Temmink) [*sic*]	Rep. of Guinea	Africa
	Otomys tropicalis	D. Rep. of the Congo	Africa
	Praomys jacksoni (de Winton)	Central African Rep.	Africa
	Praomys tullbergi (Thomas)	Nigeria	Africa
	Praomys sp.	Gabon	Africa
	Rattus norvegicus Berkenhout	Egypt, Rep. of Guinea, Jamaica, Philippines, Costa Rica, Venezuela	Africa, Caribbean, SE Asia, Central America, South America
	Rattus rattus Linnaeus	Egypt, Nigeria, Central African Rep., Jamaica, Taiwan	Africa, Caribbean, SE Asia
	'Rat'	Guyana	South America
	Tatera kempi Wroughton	Nigeria	Africa
	Tatera sp.	D. Rep. of the Congo	Africa
	Uranomys ruddi Dollman	Nigeria	Africa
Sciuridae	*Xerus erythropus* (Desmarest)	Nigeria	Africa
	Funisciurus anerythrus Thomas	Nigeria	Africa
	Funisciurus leucogenys (Waterhouse)	Nigeria	Africa
	Heliosciurus rufobrachium (Waterhouse)	Nigeria	Africa
Lorisidae	*Perodicticus potto* (Müller)	Nigeria, Gabon	Africa

Table 1 continued

Host		Distribution	
		Location	Region
Cebidae	*Cebus capucinus* Linnaeus	Panama	Central America
	Aotus lemurinus Geoffroy	Panama	Central America
	Ateles fuscieps Gray	Panama, France	Central America, Europe
	Ateles ater (Cuvier) [*sic*]		
Pongidae	*Pan troglodytes* (Blumenbach)	Tanzania	Africa
Erinaceidae	*Hemiechinus auritus* (Gmelin)	Egypt	Africa
Viverridae	'Mongoose'	D. Rep. of the Congo	Africa

Data from: Gedoelst, 1916; Ortlepp, 1924; Baylis, 1928; Joyeux et al., 1928; Brumpt, 1931; Tubangi, 1931; Foster & Johnson, 1939; Dollfus & Chabaud, 1955; Morel, 1959; Myers & Kuntz, 1960; Quentin, 1969; Campos & Vargas, 1978; Ashour, 1980; Scharff et al., 1993, 1997; Behnke et al., 2000; Asakawa & Nicolas, 2003; Tenora et al., 2003; Petrzelkova et al., 2006; Waugh et al., 2006; this study

by passage through flour beetles *Tribolium confusum* and laboratory mice *Mus musculus* BKW strain (see Lowrie et al., 2004). Passaged worms were collected at 60 days, 89 days and at an unknown date post-infection, fixed in Berland's fluid and stored in 85% alcohol. The type-specimens and additional material housed in the Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (KMMA) were examined for comparative purposes.

Specimens were cleared in lactophenol and examined as wet mounts. Hand-cut sections of the anterior end were mounted, *en face,* in polyvinyl lactophenol and posterior ends of selected males were mounted in Berlese's fluid to demonstrate spicule morphology. Drawings were made with the aid of a drawing tube attached to an Olympus BH2 microscope and measurements, in micrometres unless otherwise stated, taken using an ocular micrometer, are given as the range followed by the mean in parentheses. Statistical analysis of each of the measurements was carried out by general linear modelling (GLM) in SPSS (vers. 12.0.1) with sex and site of collection as factors (dependent variables) and worm length as a covariate to control for differences in overall size when assessing other morphometric features. Tukey's HSD *a posteriori* test was used to distinguish between the levels within each factor (e.g. specific sites within the factor site) responsible for the overall significant effect.

Specimens have been deposited in the South Australian Museum, Adelaide, Australia (SAM). Host names follow Barome et al. (2001).

Results

No differences were found in the morphology of *Protospirura muricola* collected from *Acomys dimidiatus* from any sites in the vicinity of St Katherine or in *P. muricola* passaged through more than 20 generations (over 10 years, 1997–2007) using laboratory mice (Table 2). There were, however, some statistically significant differences in the morphometrics of the populations studied, even when the effect of the sex of the worms was taken into account. Both the largest and smallest males and smallest females were found amongst the passaged worm populations. Mean lengths, 21 mm for males and 35.5 mm for females, of passaged worms were within the range of mean lengths for worms from field collections; these were 15 mm and 27.5 mm respectively for Wadi El Arbaein, 17 mm and 35.8 mm respectively for Wadi Gharaba and 29.1 mm and 39.1 mm respectively for Wadi Tlah. The differences in worm length between wadis, with sex taken into account, were significant (model excluding passaged worms, main effect of site $F_{2,38} = 8.3$, $P < 0.001$, model $R^2 = 78.5\%$). Worms from Wadi El Arbein were smaller than those from Wadis Itlah and Gharaba. A range of other characters did not vary between populations, when controlled for the effect of worm length. However, differences were noted between the wild worm populations and those cultured in laboratory mice. In particular, the positions of the deirids and nerve-ring of cultured worms were significantly further from the anterior end than those from wild worms, even after taking

Table 2 Comparative measurements (in micrometres unless otherwise stated) of *Protospirura muricola* from *Acomys dimidiatus* at three localities in Egypt during 2004 and from Egyptian sources passaged through *Mus musculus* during 2007

	Wadi Tlah		Wadi Gharaba		Wadi El Arbaein		Laboratory culture	
	Male n = 14	Female n = 12	Male n = 9	Female n = 9	Male n = 2	Female n = 2	Male n = 8	Female n = 13
Length mm	19–26	33–44	13–25	23–45	13–17	25–30	9–30	20–42
Width	460–800	612–1290	375–680	560–1190	390–530	680–800	505–715	560–1020
Pharynx	66–135	85–175	60–115	73–135	70–83	110–115	95–115	102–140
Muscular oesophagus	260–335	290–550	235–325	335–400	235–310	315–330	230–370	300–370
Glandular oesophagus (mm)	3.6–4.9	4.4–6.5	2.3–4.3	2.1–6.7	3.1–3.4	4.7–4.8	2.8–5.4	5.1–6.3
Deirid from ant. end	205–325	265–430	240–330	255–335	245–287	265–300	270–435	355–435
Nerve-ring from ant. end	302–430	330–470	297–425	315–470	285–355	330–445	365–525	380–500
Excretory pore from ant. end	402–522	435–595	290–610	470–635	410–475	482	525–695	480–635
Left spicule	290–500		370–550		290–380		390–480	
Right spicule	268–430		310–415		260–310		390–410	
Gubernaculum	83–147		109–120		100–135		85–135	
Vulva to post. end (mm)		13.6–20.4		12.0–17.9				11.5–19.7
Egg		–		53–57 × 40–43		53–75 × 39.5–43		49.5–53 × 39.5–43
Tail length	270–515	340–630	205–490	340–560	154–290	335–375	400–425	475–630

worm lengths into consideration (in both cases there was no effect of sex nor any interactions involving sex in full factorial models with length as a covariate, so models were re-run with just site as the factor and worm length as a covariate; the main effects of site for deirids $F_{3,55} = 31.1$, $P < 0.001$, model $R^2 = 64.9\%$, and for nerve-ring $F_{3,58} = 11.2$, $P < 0.001$, model $R^2 = 46.9\%$). The position of the excretory pore was also further from the anterior end in passaged worms ($F_{3,50} = 12.9, P < 0.001$, model $R^2 = 48.5\%$). There were no apparent differences between the morphometrics of *P. muricola* collected in this study from *A. dimidiatus* and *P. muricola* from those hosts and localities reported in the literature (Table 3), although no very large females were found in the population of worms from Egyptian hosts. A complete redescription of *P. muricola* based on specimens from wild caught *A. dimidiatus* is given below.

Family Spirurida Oerley, 1885
Genus *Protospirura* Seurat, 1914

Protospirura muricola Gedoelst, 1916
Syn *P. bonnei* Ortlepp, 1924

Type-host: 'Rat', possibly *Cricetomys gambianus* Waterhouse.

Type-locality: Kivu, Democratic Republic of the Congo.

Type-material: One female and posterior end of 1 male; coll. Carlier; Koninklijk Museum voor Midden Afrika, 15437.

Material examined

Ex *Acomys dimidiatus* (Desmarest): 15 males, 18 females, Wadi Tlah (SAM AHC34820, AHC34823, AHC34826, AHC34827); 9 males, 10 females, Wadi Gharaba (SAM AHC34824, AHC34825,); 4 males, 3 females, Wadi El Arbaein (SAM AHC34828, AHC34829); Saint Katherine Protectorate, Sinai Desert, Egypt.

Ex *Mus musculus,* laboratory mice: 8 males, 13 females (SAM AHC34830), Nottingham University, UK.

Ex *Mastomys coucha* (Smith): 3 anterior ends, Elizabethville, Democratic Republic of the Congo (KMMA 30194).

Ex *Otomys tropicalis* Thomas: 9 males, 1 female, Ituri and Djuga, Democratic Republic of the Congo (KMMA 15425, 15436).

Ex *Tatera* sp.: 1 posterior end male, 1 female, Elizabethville, Democratic Republic of the Congo (KMMA 31085).

Ex 'mongoose': 1 male, Ibembo, Democratic Republic of the Congo (KMMA 27671).

Ex *Perodicticus potto* (Müller): 2 males, 3 females, Makoku, Gabon (KMMA 35481).

Description (Figs. 1–12; Table 2)

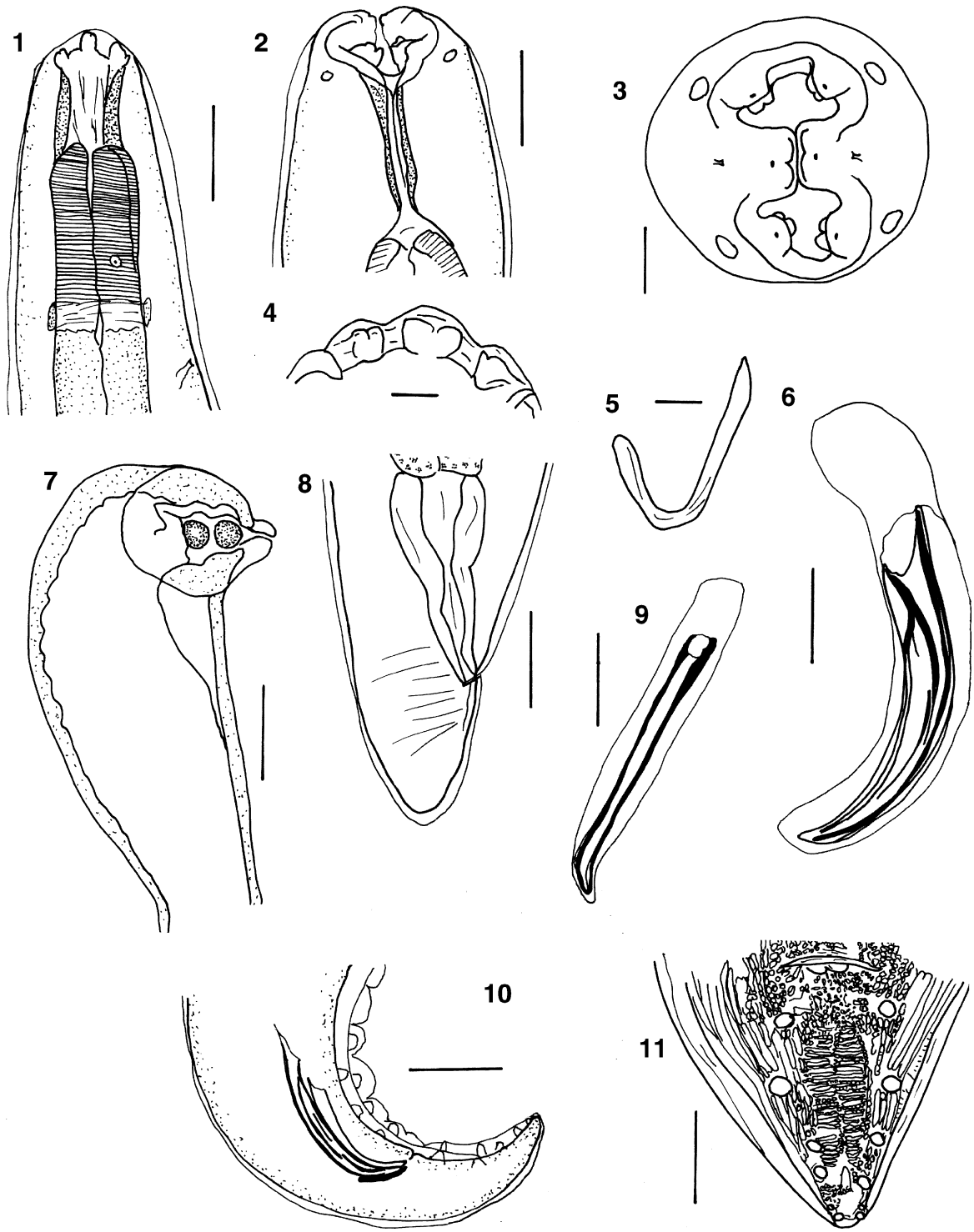
Large stout worms. Cuticle thick, with transverse striations. Anterior extremity with mouth opening dorso-ventrally elongated, surrounded by 2 highly developed tri-lobed pseudolabia, each divided into single large lateral and 2 smaller submedian lobes; each lobe with 2 denticles. Denticles on lateral lobes plate-like, on submedian lobes triangular or digitiform. Cephalic papillae arranged as 6 small labial papillae, 1 on each lobe, forming inner circle; 4 large submedian papillae and 2 amphids on lateral lobes, forming outer circle. Pharynx with thin sclerotised walls, laterally compressed. Oesophagus divided into short anterior muscular and long posterior glandular portions. Nerve-ring surrounds muscular portion of oesophagus close to junction between muscular and glandular portions. Deirids small, anterior to nerve-ring; excretory pore posterior to nerve-ring, at level of anterior limit of glandular portion of oesophagus.

Male [based on 15 specimens]. Length 19–26 (22.2) mm; width at mid body 460–800 (633). Pharynx 66–135 (111); muscular oesophagus 261–335 (306); glandular oesophagus 3,570–4,930 (4,068) long. Deirids 205–330 (284), nerve-ring 301–429 (365) and excretory pore 402–522 (455) from anterior extremity. Caudal alae relatively thick; postero-ventral surface heavily ornamented with longitudinal striae and irregular bosses pre-anally and with both longitudinal and transverse striae plus irregular bosses post-anally. Spicules dissimilar, sub-equal to equal in length; left spicule larger, 290–501 (411) long, more heavily sclerotised; right spicule 268–430 (352) long, slender; each spicule enclosed in a transparent sheath visible when spicule is extended from cloaca; sheath of left spicule more voluminous. Gubernaculum sclerotised, triangular in ventral view, 82.5–147 (112) long. Usually 10 paired and 1 unpaired caudal papillae; 4 pairs, pre-anal, large; 6

Table 3 Comparative measurements of *Protospirura muricola* from a range of rodent host species and a primate from the localities listed

	Kenya		Nigeria		Philippines		Panama		Guyana		Central African Rep.		Egypt	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Length mm	31	50	15–25	20–50	25–30	35–52	25–40	40–70	25	44	20–27	20–51	13–26	22–45
Width	800	1,260	450–470	900–1,200	800	1,200	580–675	780–1,200	760	1260	530–650	350–1,900	375–800	597–1,300
Pharynx		160	130–160		90	100–130	130–136	145–150			110–135	125–160	60–135	73–175
Oesophagus (mm)		7.5	3.5–4.3		6.2	6.4–7.9	5.5	7.0			3.1–4.1	1.8–5.4	2.5–5.3	4.7–7.0
Deirid from ant. end			310–320		320–335	330–400	315–350	360–385		234	220–250	230–260	205–330	245–430
Nerve-ring from ant. end		280	330–400		380–410	380–470	350–385	410–470			270–370	280–410	285–430	315–470
Excretory pore from ant. end		630	440–600		430–450	480–700	490–535	560–675			360–410	360–520	288–610	435–637
Left spicule	480		430–520		430–450		525		395		475–555		290–550	
Right spicule	350		350–400		360–390		434		395		450–520		260–430	
Gubernaculum	128				100		134						83–147	
Egg		48–56 × 40		50–37		50–57 × 38–44		53 × 40		47–51 × 37–39				49.5–76 × 39.5–43
Vagina from post. end (mm)		22.2								9.0–27.0		6–25.0		11.5–20.4
Tail length	450	400			420	400–420		460–550			400–520	245–435	154–515	335–630

Data are taken from: Gedoelst, 1916; Ortlepp, 1924; Baylis, 1928; Tubangi, 1931; Foster & Johnson, 1939; Quentin, 1969; this study



Figs. 1–11 *Protospirura muricola* Goedelst, 1916. 1. Anterior end of female, lateral view. 2. Anterior end of male, dorso-ventral view, 3. Male, *en face* view. 4. Pseudolabium of female, internal view. 5. Gubernaculum, ventral view. 6. Left spicule, 7. Distal vagina and vulva, dissected from body, lateral view. 8. Female tail, lateral view. 9. Right spicule. 10. Male posterior end, lateral view. 11. Male tail, ventral view. *Scale-bars*: 1,2,6,7,9, 100 μm; 3, 50 μm; 4,5, 25 μm; 8,10,11, 200 μm

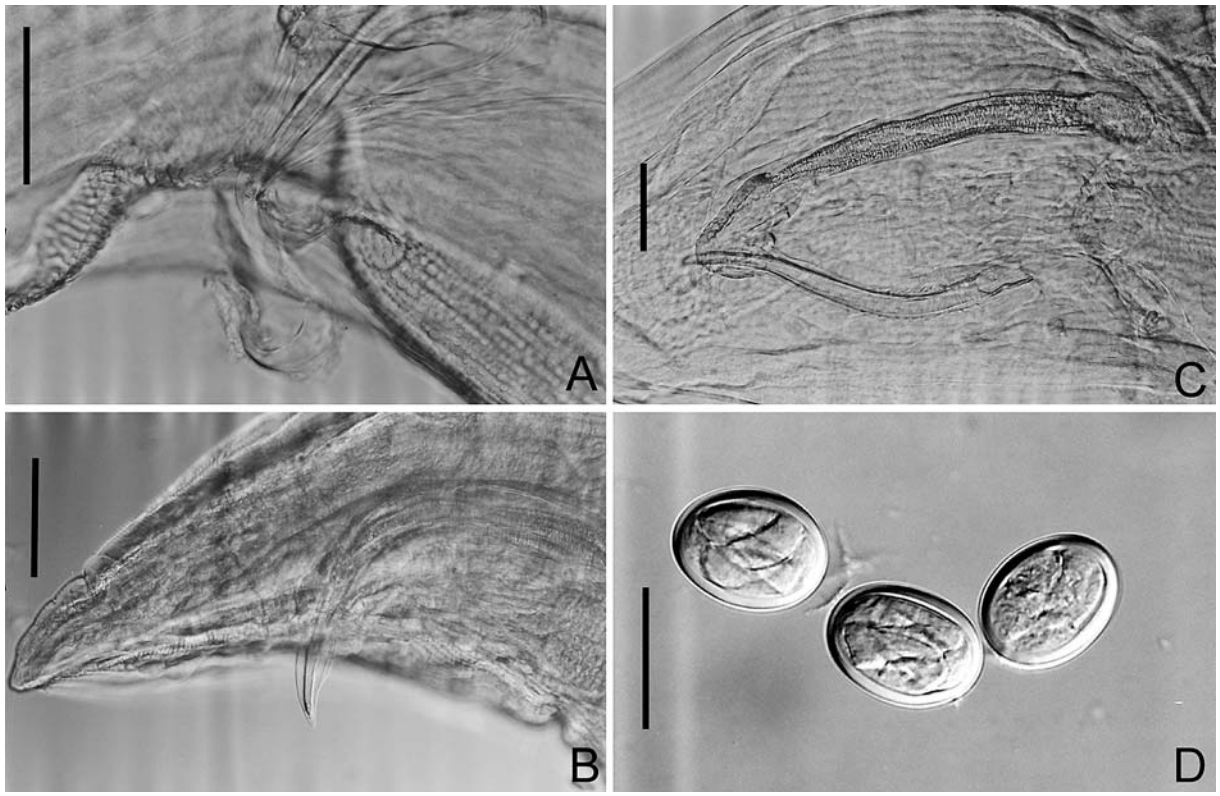


Fig. 12 *Protospirura muricola* Goedelst, 1916. A. Posterior of end male, lateral view. B. Posterior end of male, lateral view. C. Spicules and gubernaculum *in situ*, ventral view. D. Eggs. *Scale-bars*: A,D, 50 μm; B,C, 100 μm

pairs post-anal, of which first 2 pairs large, next 2 pairs smaller and posterior-most 2 pairs smallest, clustered near tail tip. Tail conical 270–516 (400.5) long.

Female [based on 17 specimens]. Length 35–45 (42) mm; width at mid-body 612–1290 (1190). Pharynx 83–174 (117); muscular oesophagus 288–549 (378.5); glandular oesophagus 4,420–6,680 (5,600) long. Deirids 254–429 (322), nerve-ring 330–469 (426) and excretory pore 435–636 (511) from anterior extremity. Vulva without ornamentation, 12.7–20.4 (18.1) mm from posterior extremity, in posterior half of body; vagina directed posteriorly. Tail conical 340–629 (495) long. Eggs elliptical, embryonated, 49–59 (56.1) × 40–46 (41.5).

Remarks

At present 10 species of *Protospirura* are recognised as valid (Hasegawa, 1990; Smales, 2001). Of these, *P. numidica* Seurat, 1914, *P. anopla* Kreiss 1938, *P. armenica* Alojan, 1951, *P. chabaudi* Vuylsteke, 1964, *P. okinavensis* Hasegawa, 1990, *P. peromysci* Babero & Matthias, 1967 and *P. suslica* Schultz, 1916 all have four denticles on each lateral lobe of the pseudolabia. *P. muricola,* however, is one of three species that have only two denticles on each lateral lobe. With six pairs of post-anal papillae, a slender, slightly shorter right spicule and the vulva opening in the posterior half of the body, *P. muricola* differs from *P. pseudomuris* Yokohata & Abe, 1989, which also has six pairs of post-anal papillae, but which has the right spicule twice as long as the left and the vulva in the anterior third of the body (Yokohata & Abe, 1989), and from *P. kaindiensis* Smales, 2001, which has only five pairs of post-anal papillae, a slender, shorter left spicule and the vulva in the anterior third of the body (Smales, 2001).

No significant differences were found in the morphology of the specimens from a range of hosts held in the KMMA. Nor were there significant

differences in the morphology of populations of *P. muricola* collected from *A. dimidiatus* in the semi-isolated wadis around St Katherine (Table 2). There is no suggestion from the morphometrics of the worms (Table 3) that sub-populations of *A. dimidiatus* might be sufficiently geographically structured to favour the evolution of distinct genetic variants of *P. muricola,* although hosts from differing localities harboured varied helminth communities (Behnke et al., 2004). The differences in lengths were most probably due either to the ages of the worms when collected, which could not be determined with certainty for either the wild caught or passaged worms, and/or to density-dependent effects on morphometry, as reported by Lowrie et al. (2004), for passaged worms. In his study of a large number of specimens from more than 17 host species, Baylis (1928) noted that Gedoelst's (1916) type-specimens were above average in size. Subsequently, other populations of large worms have been reported; for example, from captive monkeys in Panama (Foster & Johnson, 1939).

The statistically significant differences in the position of the deirids, nerve-ring and excretory pore between cultured and wild caught worms in this study may be the result of the different fixatives used. Fixation of wild caught worms was carried out using formalin at room temperature, which does not encourage them to straighten to their full length and causes shrinkage (Fagerholm & Lövdahl, 1984), whilst Berland's fluid, used for cultured worms, does enable straightening does not cause shrinkage; consequently measurements of organs from the anterior end may differ between specimens. It is also possible, however, that the differences between these worms were due to host-induced differences (*Acomys* and *Mus* are not closely related) or were due to founder effects because of the small number of worms used to begin the laboratory colony.

The left spicules of individuals from the El Arbaein population were shorter than those from other sites (Table 2) and the Egyptian populations had shorter spicules than has been reported from *P. muricola* from other hosts (Table 3). Worms with the shortest spicules were, however, not necessarily the smallest individuals. Wertheim (1962), in her study of *Mastophorus muris,* noted that spicule length bore no constant relation to body length, while Read & Millemann (1953) suggested that absolute spicule length may be variable in *Mastophorus* and *Protospirura*. This seems to be the case here.

Discussion

Understanding the morphology of the pseudolabia of *Protospirura muricola* and its congeners has been confounded both by the taxonomic uncertainty discussed above and the range of terminology used to describe the tooth-like elements on the inner aspect of the lobes. Wertheim (1962), however, demonstrated that differences in 'tooth structure', amongst other characters, clearly separate *Mastophorus* and *Protospirura.* Each lobe of the pseudolabium of *Mastophorus* has a 'tooth' on its internal surface consisting of a variable number of serrations of the anterior aspect of a thin flexible membrane (Wertheim, 1962). In contrast the 'teeth' of species of *Protospirura* consist of paired triangular or digitiform elements, formed from cuticular extensions, on each of the submedian lobes and two or four flattened cuticular plates on each of the lateral lobes (see for example Baylis, 1928; Babero & Mathias, 1967; Quentin et al., 1968; Quentin, 1969; Yokohata & Abe, 1989; Hasegawa, 1990). When Scharff et al. (1993) examined the head morphology of *P. muricola* using scanning electron microscopy, they interpreted the inner surface of each lateral lobe of the pseudolabium as a median inner pseudolabium without tooth-like elements. However, the images of the cephalic ends presented by them (their figure 1B,D) show the tips of two cuticular plates similar to figures 161, 162 in Ashour (1980). The term denticle seems an appropriate descriptor for these tooth-like elements given that they are cuticular in origin, are associated with the mouth opening and are not teeth as such.

Another source of confusion has been in the use of spicule morphology as an informative character to distinguish species, because descriptions of the spicules have varied between authors (see for example Gedoelst, 1916; Ortlepp, 1924; Baylis, 1928; Tubangi, 1931; Quentin, 1969; Asakawa & Nicholas, 2003; Petrzelkova et al., 2006). In most of the populations of *P. muricola* that have been studied, the left spicule is more robust, broader, more heavily sclerotised and slightly longer than the right. In some instances, however, the spicules are of equal length

and with only small differences in shape (Ortlepp, 1924; Quentin, 1969). Yokohata & Abe (1989) reported some variation in spicule shape in a few individuals of *P. pseudomuris*; in one instance both spicules were long and narrow and in others both spicules were short and wide. These are similar to the differences in the description of the spicules given for *P. muricola*. The wide delicate expansions of the ala described by Baylis (1928) and Foster & Johnson (1939), and figured by Quentin *et al*. (1968), appear rather to be a transparent sheath, clearly apparent when the spicule is extended from the cloaca and was noted in the material from the KMMA. This sheath is also visible in adequately fixed specimens when the spicules are *in situ* within the body. In one instance in this study a sheath was seen protruding from the cloaca without the enclosed spicule (Fig. 12A). A similar element was described and figured for *P. pseudomuris* (see Yokohata & Abe, 1989), suggesting that such a spicule sheath may be a feature of *Protospirura* which is only easily detected in males when the spicule is extended. A similar, but narrower, sheath covers the right spicule.

P. muricola is primarily a parasite of murid rodents (25 species, including *Rattus norvegicus* and *R. rattus*) in Africa. It has also been reported from bathyergid rodents (two species), sciurid rodents (four species) and, possibly accidentally, in a carnivore, an insectivore and primates (Table 1). Baylis (1928) noted that it was the most common nematode infecting Nigerian rodents. Experimental and field studies have shown that the life-cycle of *P. muricola* can be completed in a range of insect hosts, such as beetles, dermapterans and cockroaches, including the cosmopolitan *Leucophaea maderae* (Fabricius) (Anderson, 2000; Lowrie et al., 2003).

The only reports of *P. muricola* occurring outside Africa are infections in the cosmopolitan rodents, *R. norvegicus* and *R. rattus,* and in captive primates. In most cases infected the cockroach *L. maderae* was associated with these hosts (Brumpt, 1931; Foster & Johnson, 1939; Campos & Vargas, 1978). Since *R. norvegicus* probably originated in northern China and *R. rattus* in Malaysia (Nowak, 1991), they may both have acquired *P. muricola* after arrival in Africa. The spread of *P. muricola* beyond Africa could then have been linked to the migration of infected *Rattus* species and the proximity of cosmopolitan cockroach species. Black or brown rats may also have acquired *P. muricola* from infected cockroaches in locations outside of Africa where they are sympatric. Unwitting human assistance could have assisted this process. The spider monkey, which died in the Menagerie du Museum, Paris some time after capture in northern South America (Dollfus & Chabaud, 1955), may have been infected with *P. muricola* prior to its arrival in Europe. This report appears to be the only known instance of *P. muricola* occurring in Europe.

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