

# Description of *Proyseria petterae* n. sp., with an amended generic diagnosis and a review of the species of *Proyseria* Petter, 1959 and *Stegophorus* Wehr, 1934 (Nematoda: Acuariidae)

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**Abstract** *Proyseria decora* (Dujardin, 1845) (the type-species of the genus *Proyseria* Petter, 1959) is redescribed on the basis of specimens from *Alcedo atthis* (L.) (Coraciiformes: Alcedinidae) from Iran. *P. petterae* n. sp. is described from *Corythornis vintsioides* (Eydoux & Gervais) (Alcedinidae) from Madagascar by light and scanning electron microscopy. *Proyseria* sp. from *Alcedo euryzona* Temminck from continental Malaysia is described on the basis of a single male specimen. *Stegophorus alcedonis* Puqin, Yanyin & Guocal, 1991 from *A. atthis* in China is transferred to the genus *Proyseria* as *P. alcedonis* n. comb. The generic diagnosis of *Proyseria* is amended. Review of the species of the genera *Proyseria* and *Stegophorus* Wehr, 1934 is presented.

## Introduction

The genus *Proyseria* Petter, 1959 was erected as monotypic for *Proyseria decora* (Dujardin, 1845) (= *Dispharagus decorus* Dujardin, 1845), a parasite of common kingfisher, *Alcedo atthis* (L.) and then known from France and Iran (Dujardin, 1845; Chabaud 1953; Petter, 1959). Subsequently, it was reported from the same host in the Russian Far East (Oshmarin, 1963) and Vietnam (Ryzhikov & Khokhlova, 1964). Our recent surveys of helminth parasites of kingfishers from Malaysia and Madagascar have revealed that the genus *Proyseria* is more diverse and has a wider geographical range than previously known.

The aim of the present study is to describe newly-collected specimens of *Proyseria* from Malaysia and Madagascar. In addition, we review the species of the related genus *Stegophorus* Wehr, 1934 and propose an amended generic diagnosis of *Proyseria*.

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## Materials and methods

During field trips by two of the present authors (JM and BBG), three *Alcedo euryzona* Temminck (Coraciiformes: Alcedinidae) in Selangor, Malaysia (10 August 2010) and two *Corythornis vintsioides* (Eydoux & Gervais) (Coraciiformes: Alcedinidae) at Sahambaky, Madagascar (22–23 October 2013) were captured by mist nets and dissected immediately after their death. Nematodes collected under the koilin lining of the

gizzard were fixed and stored in 70% ethanol. Voucher material of *Proyseria decora* (Dujardin, 1845) studied by Chabaud (1953) and Petter (1959) from the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN), no. 527A, was re-examined.

For light-microscopical observations, specimens were cleared and examined as temporary mounts in lactophenol. A single female specimen from *C. vintsioides* used for scanning electron microscopy (SEM) observations was dehydrated in an ethanol series, immersed in hexamethyldisilazane for 20 min, air-dried, coated with gold in a Cressington 108-Auto coater and examined using a Zeiss DSM 940A microscope at 10 kV. All measurements are in micrometres unless otherwise stated. Metrical data are given as the range, with the mean and the number of measurements taken (n) in parentheses unless otherwise indicated. The following indices were used:  $I_{mOE/gOE}$ , length of muscular oesophagus/length of glandular oesophagus;  $I_{OE/BL}$ , length of oesophagus/body length;  $I_{LSP/RSP}$ , length of left spicule/length of right spicule.

DNA was extracted from mid-body portion of a single female specimen, whose body extremities were used for SEM study, and dissolved in 100 µl TE buffer. A fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified using a reverse primer 5'-AAT AAG TAC GAG TAT CAA TAT C-3' (Casiraghi et al., 2001) and forward primer 5'-TGA TTG GTG GTT TTG GTA ATT G-3' from the same study, elongated with three nucleotides at the 3'-end. PCR reaction was performed in a final volume of 50 µl containing 1× CoralLoad PCR buffer (Qiagen), 0.2 mM of each dNTP, 10 pmol of each primer, 1.5 U Taq polymerase (Qiagen) and 1 µl of DNA extract. The PCR cycling conditions were: 94°C for 1 min followed by 5 cycles (94°C for 50 s, 47°C for 50 s and 72° for 60 s), followed by 30 cycles (94° for 50 s, 50° for 50 s, 72° for 60 s), followed by a final extension step at 72°C for 5 min. Sequencing was performed by MacroGen Inc. using the amplification primers.

The newly-collected materials described in this study are deposited in the Natural History Museum of Geneva (MHNG).

### *Proyseria petterae* n. sp.

*Type-host*: *Corythornis vintsioides* (Eydoux & Gervais) (Coraciiformes: Alcedinidae).

*Type-locality*: Sahambaky, Madagascar (19°3'54"S, 48°20'25"E).

*Site in host*: Under the koilin lining of the gizzard.

*Prevalence*: In two out of two host individuals studied.

*Intensity of infection*: 1–3 (mean 2).

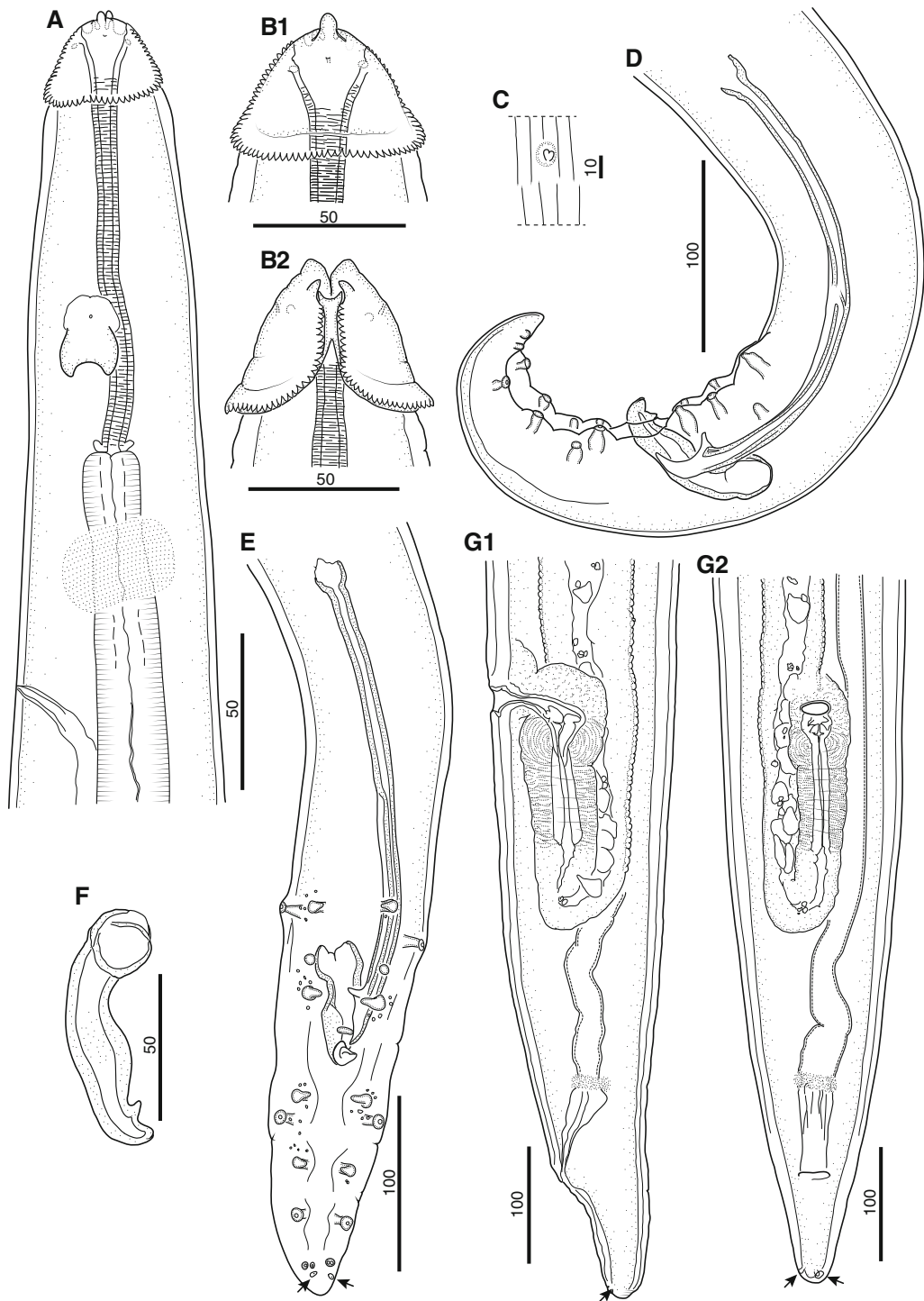
*Type-specimens*: Holotype: MHNG-INVE-87381 (1 male). Paratypes: MHNG-INVE-87382 (2 females); MHNG-INVE-87384 (anterior and posterior fragments of 1 female, SEM stub).

*Etymology*: The new species is named for Dr A. Petter, Muséum National d'Histoire Naturelle, Paris, in recognition of her contribution to the taxonomy of this nematode group.

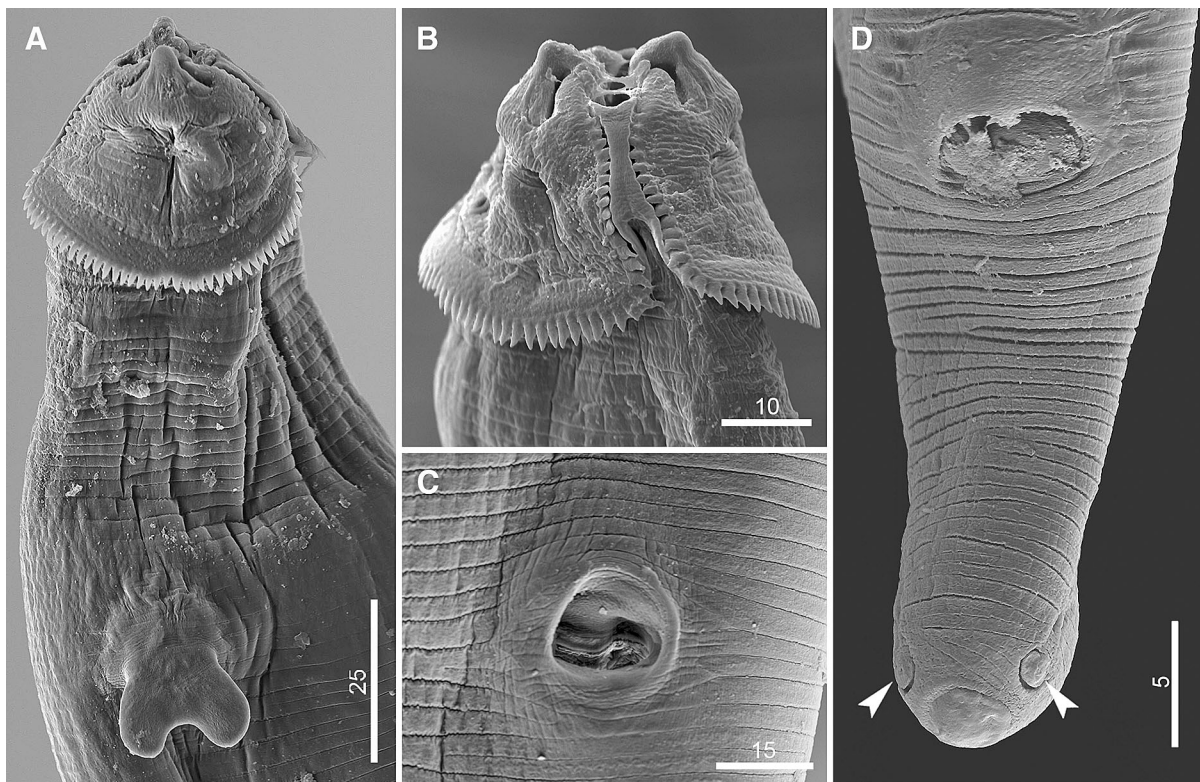
### Description (Figs. 1, 2)

*General*. Small-sized acuariid nematodes with thin body. Anterior end with 2 pseudolabia, each of them with prominent apex and bearing single amphid and pair of inconspicuous cephalic papillae (Figs. 1A, B, 2A). Cuticular ornamentation present in form of denticulate collarete formed by 2 halves, each of them posterior to pseudolabium (Figs. 1A, B, 2A). Sublabia differentiated between pseudolabia (Figs. 1B2, 2B). Body cuticle thick, with distinct transverse striations interrupted along lateral body line. Deirids large, bicuspid, situated at level anterior to junction of buccal cavity and muscular oesophagus. Postdeirids bifurcate, each situated in shallow pit (Fig. 1C). Buccal cavity long, with conspicuous cross-striations. Muscular and glandular portions of oesophagus distinct. Glandular oesophagus and intestine with similar width at their junction. Nerve-ring surrounds anterior portion of muscular oesophagus. Excretory pore posterior to nerve-ring (Fig. 1A). Phasmids subterminal (Figs. 1E, G, 2D).

*Male* (n = 1). Body 4.35 mm long. Maximum body width 125 at mid-length, 65 at level of cloaca. Tail 133 long. Cuticle 6 thick, with transverse striations 7–8 apart. Collarete 31 long, 41 wide in lateral view, each half bears 56 cusps, *c.* 3 long. Deirids 18 long, 18 wide, situated at 104 from anterior extremity. Left and right postdeirids situated at 0.58 mm and 1.33 mm, respectively, from posterior extremity. Excretory pore at 219 from anterior extremity. Buccal cavity 135 long, 8 wide. Muscular oesophagus 685 long, 33 wide at mid-length, with maximum width 36 at posterior end. Glandular oesophagus 1,482, with maximum



**Fig. 1** *Proyeria petterae* n. sp. A, Anterior end, male, lateral view; B, Cephalic region, female, lateral (B1) and dorsoventral (B2) view; C, Postdeirid, female; D, Posterior end, male, sinistral view; E, Posterior end, male, ventral view, note phasmids (arrows); F, Right spicule, dextral view; G, Posterior extremity, female, sinistral (G1) and ventral (G2) view, note phasmids (arrows). Scale-bars are in micrometres



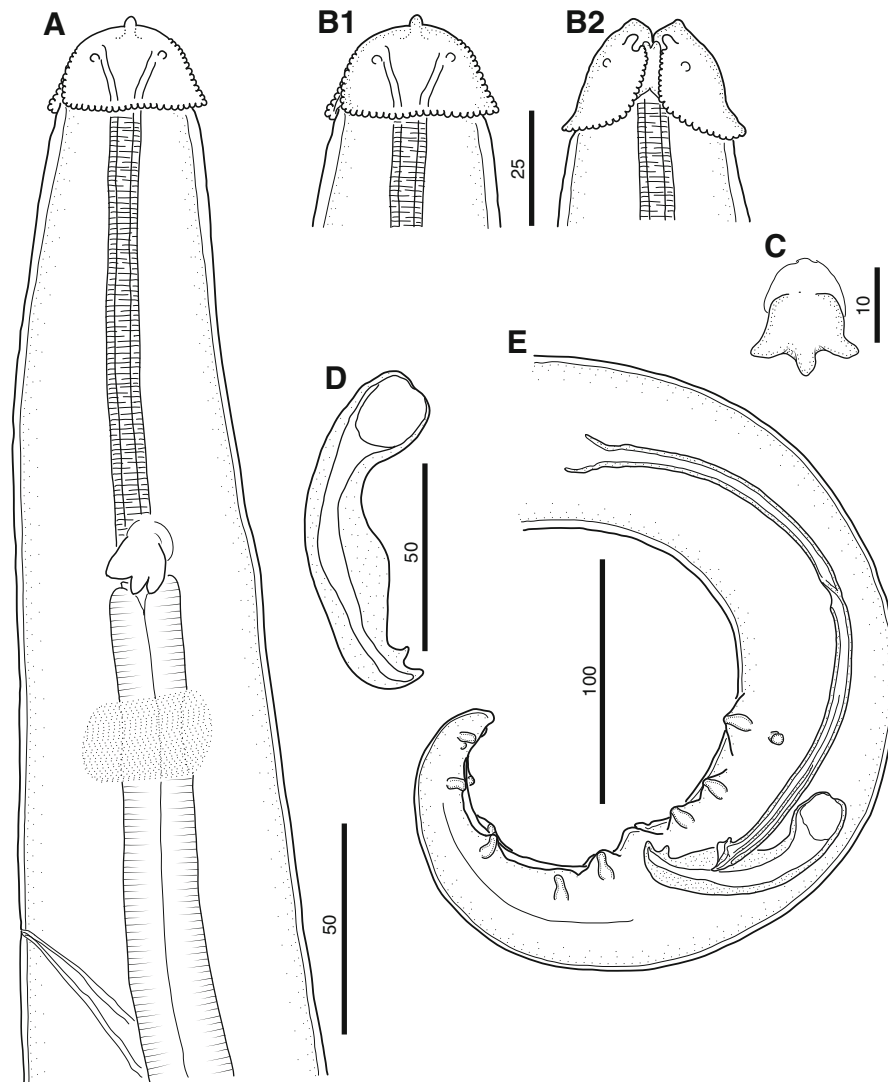
**Fig. 2** *Proyseria petterae* n. sp., female, scanning electron micrographs. A, Anterior end, lateral view; B, Cephalic region, dorsoventral view; C, Vulva; D, Posterior end, ventral view, note phasmids (arrowheads). Scale-bars are in micrometres

width at mid-length 77. Nerve-ring at 165 from anterior body end. Testis reflection at 2.28 mm from anterior end. Caudal alae slightly developed, 251 long (Fig. 1D, E). Preloacal papillae represented by single ventral preloacal papilla and 4 pairs of pedunculate papillae: pairs 1, 3 and 4 subventral, pair 2 displaced in lateral direction. Postloacal papillae 6 pairs: 5 subventral pedunculate pairs and 1 pair of small papillae situated between bases of last pair of subventral papillae. Left spicule 289 long, composed of handle, 146 long, and blade, 143 long (Fig. 1E). Right spicule robust, 92 long, with 2 prominent distal cusps (Fig. 1F).

*Female* (n = 2; measurements of one of specimens are followed by those of the second one in parentheses). Body 8.27 (8.35) mm long, with maximum body width at mid-body, 188 (247); body width at level of vulva 155 (197), at level of anus 73 (80). Collarete 46 (48) long, 65 (68) wide in lateral view, each half bears 70–72 cusps, 4–5 long. Deirids 24–26 long, 28–29

wide situated at 147 (155) from anterior extremity. Left and right postdeirids situated at 2.10 (2.33) mm and 2.73 (3.26) mm, respectively, from posterior extremity. Excretory pore at 297 (309) from anterior extremity. Buccal cavity 172 (188) long, 10–12 wide. Muscular oesophagus 1,013 (961) long, 42 (43) wide at mid-length and 59 (54) at its posterior end. Glandular oesophagus 2,140 (2,246) long, with maximum width at mid-length 93 (90). Cuticle 22–23 thick, with transverse striations, 6 apart. Vulva (Figs. 1G, 2C) at 498 (499) from posterior extremity. Vagina directed posteriorly, composed of *vagina vera*, 74 (74) long, separated by sphincter from *vagina uterina*, 101 (104) long, with thick muscular walls. Reproductive system monodelphic. Tail 105 (107) long, with rounded tip (Figs. 1G, 2D).

*Molecular identification.* A fragment of 646 bp of the COI gene was amplified. The nucleotide sequence is available in the GenBank database (KJ995862).



**Fig. 3** *Proyseria decora*, male. A, Anterior end, male, lateral view; B, Cephalic region, lateral (B1) and dorsoventral (B2) view; C, Deirid; D, Right spicule, dextral view; E, Posterior end, sinistral view. Scale-bars are in micrometres

#### Remarks

By having bicuspid deirids, *Proyseria petterae* n. sp. differs from its two congeners, *P. decora* and *P. alcedonis* (Puqin, Yanyin & Guocal, 1991) n. comb., which possess tricuspid deirids. In addition, the male of the new species has collarette, each half of which is armed with 56 pointed cusps (Fig. 1A), while those of *P. decora* are 46–48 in number and rounded (Fig. 3B) (see below). *P. alcedonis* has a cuticular collar situated almost equidistantly between the posterior rim of the collarette and the deirids, as

described by Puqin et al. (1991); a collar is absent in the new species.

#### *Proyseria decora* (Dujardin, 1845) Petter, 1959

Syns *Dispharagus decorus* Dujardin, 1845; *Histiocephalus decorus* (Dujardin, 1845) Diesing, 1854; *Yseria decora* (Dujardin, 1845) Gedoelst, 1919, *Pri-onostemma decorum* (Dujardin, 1845) Gendre, 1920; *Streptocara decora* (Dujardin, 1845) Skrjabin, 1916

*Host*: *Alcedo atthis* (L.) (Coraciiformes: Alcedinidae).

*Locality*: Near the city of Chalus, Iran, October 1951.

*Site in host:* Under the koilin lining of the gizzard.

*Intensity of infection:* 3 males.

*Voucher material:* MNHN 527A.

### Description (Fig. 3)

*Male* (n = 3; except when otherwise indicated). Body 5.05–5.46 (5.17) mm long. Maximum body width 80–83 (82), posterior to oesophago-intestinal junction; body width at level of cloaca 54–58 (57). Tail 132–151 (143) long. Cuticle 3–4 thick, with transverse striation slightly distinct, 5–6 apart. Collarette, in 2 halves, 22–26 long, 35 (n = 1) wide in lateral view; each half bears 46–48 rounded cusps on its entire rim (Fig. 3A, B). Deirids tricuspid (Fig. 3A, C), about 10 long, situated at 103–110 (106) from anterior extremity. Excretory pore located at 215–229 (223) from anterior body end. Buccal cavity 123–132 (128) long, 8–9 wide. Muscular oesophagus 500–585 (547) long, 25–26 wide at mid-length. Glandular oesophagus 1,360–1,461 (1,421) long, 42–45 (44) wide at mid-length. Nerve-ring at 148–157 (151) from anterior extremity. Caudal alae slightly developed, 248–279 (261) long (Fig. 3E). Precloacal papillae represented by single, ventral, precloacal papilla and 4 pairs of papillae: pairs 1, 3 and 4 subventral, pedunculate and arranged equidistantly, second pair of papillae lateral, situated at level of first pair. Postcloacal papillae 6 pairs: 5 subventral pedunculate pairs and 1 small, sessile pair, situated between bases of last pair of pedunculate papillae. Left spicule 261–282 (270) long, composed of handle 136 (n = 1) long and blade 125 (n = 1) long (Fig. 3E). Right spicule robust, 96–98 (97) long, armed with two prominent distal cusps (Fig. 3D).  $I_{\text{mOE/gOE}}$  0.35–0.43 (0.39);  $I_{\text{OE/BL}}$  0.36–0.40 (0.38);  $I_{\text{LSP/RSP}}$  2.69–2.94 (2.79).

### Remarks

The present redescription is based on the male specimens studied by Chabaud (1953). This sample differs from the original description of *P. decora* mainly in its greater body dimensions and slightly longer spicules (Table 1). However, both samples have a similar morphology of the collarette and the position, size and shape of deirids.

Oshmarin (1963) did not provide morphometric data for the three males from *A. atthis* in the Russian Far East; however, the morphology of the anterior extremity illustrated by him resembles that of *P.*

*decora*. The record of this species from Vietnam by Ryzhikov & Khokhlova (1964) was complemented with a description published by Skrjabin et al. (1965). This material differs from the other three records in its collarette with a prominent denticulated posterior rim and deirids with three pointed cusps.

### *Proyseria* sp.

*Host:* *Alcedo euryzona* Temminck (Coraciiformes: Alcedinidae).

*Locality:* Gombak Field Station, Selangor, Malaysia (3°19'12"N, 101°45'0"E, altitude 970 m).

*Site in host:* Under the koilin lining of the gizzard.

*Prevalence and intensity of infection:* 1 male found in 3 examined birds.

*Voucher:* MHNG-INVE-87385 (1 male).

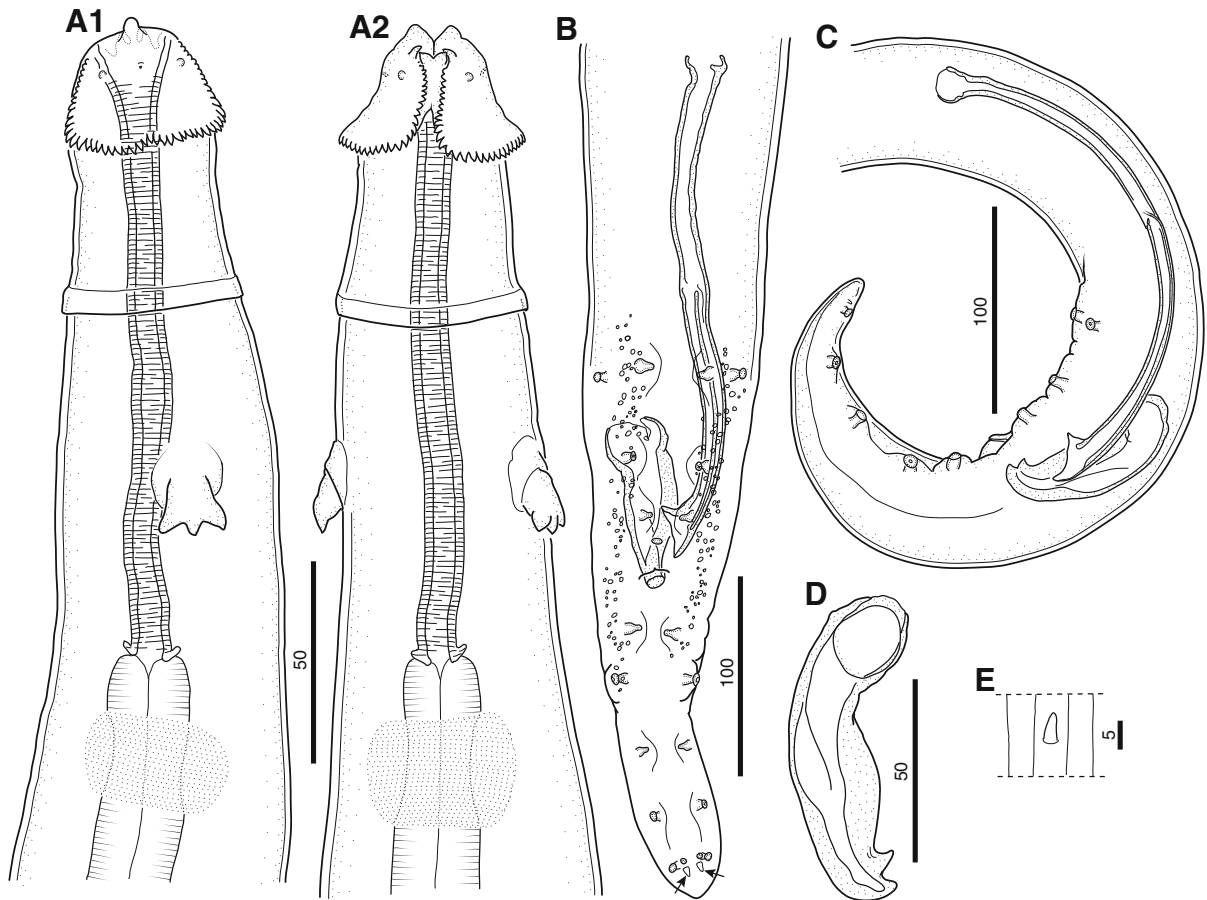
### Description (Fig. 4)

*Male.* Body 5.35 mm long. Maximum body width at level of oesophago-intestinal junction 116; body width at level of cloaca 55. Tail 166 long. Cuticle 4–5 thick, with transverse striations 5–6 apart. Collarette, formed by 2 halves, 32 long and 43 wide in lateral view; each half bears 57 cusps on its entire rim (Fig. 4A). Deirids tricuspid, 14–15 long, 17 wide, at 111 from anterior extremity. Left and right postdeirids 5 long (Fig. 4E), situated at 1,313 and 1,831, respectively, from posterior extremity. Cuticular collar 6 long, surrounds body at 70 from anterior extremity. Excretory pore at 250 from anterior extremity. Buccal cavity 151 long, 9 wide. Muscular oesophagus 649 long, 30 wide at mid-length and 45 wide at its posterior end. Glandular oesophagus 1,482 long, with maximum width 96 situated at mid-length. Nerve-ring at 165 from anterior extremity. Testis reflection at 2.75 mm from anterior extremity. Caudal alae slightly developed, 301 long (Fig. 4B, C). Precloacal papillae represented by single ventral precloacal papilla and 4 pairs of pedunculate papillae: pairs 1, 3 and 4 subventral, pair 2 displaced in lateral direction. Postcloacal papillae 6 pairs: 5 subventral pedunculate pairs and 1 small sessile pair, situated between bases of last pair of subventral papillae. Phasmids posterior to last pair of papillae. Left spicule 277 long, composed of handle 133 long and blade 144 long (Fig. 4B, C). Right spicule robust, 95 long, with 2 prominent distal cusps (Fig. 4D).

**Table 1** Metrical data of *Proyseria* spp. from various hosts and localities

Species	<i>P. alcedonis</i> n. comb.		<i>P. decora</i>		<i>P. decora</i>		' <i>P. decora</i> '		<i>P. petterae</i> n. sp.		<i>Proyseria</i> sp.
	Puquin et al. (1991)		Dujardin (1845)		Present study		Ryzhikov & Khokhlova (1965)		Present study		
Host	<i>Alcedo atthis</i>		<i>A. atthis</i>		<i>A. atthis</i>		<i>A. atthis</i>		<i>Corythornis vintisoidea</i>		<i>Alcedo euryzona</i>
Country	China		France		Iran		Russia		Madagascar		Malaysia
	Female (n = 1)		Male (n = 1)	Female (n = 1)	Male (n = 3)		Male (n = 1)	Female (n = 1)	Male (n = 1)	Female (n = 2)	Male (n = 1)
Body length (mm)	9.36		3.60	8.00	5.03–5.46		2.48	6.40	4.35	8.27–8.35	5.35
Maximum body width	256		110	200	80–82		116	224	125	188–247	116
Tail length	112		130	130	132–151		–	80	133	97–105	166
Collarete length	38		–	–	22–26		30	50	31	46	32
Distance from anterior end to deirids	122		–	–	130		76	132	104	147–155	111
Distance from anterior end to excretory pore	280		–	–	215–229		–	–	219	294–309	250
Buccal cavity length	168		–	–	123–132		40*	165	135	172–188	151
Muscular oesophagus length	560		–	–	500–585		400	640	685	961–1,013	649
Glandular oesophagus length	1,600		–	–	1,360–1,461		960	1,540	1,482	2,140–2,246	1,482
Left spicule length	–		237	–	261–282		281	–	289	–	277
Right spicule length	–		–	–	96–98		75	–	92	–	95
Distance from posterior end to vulva	480		–	500	–		–	400	–	498–499	–
Index mOE/gOE	0.35		–	–	0.35–0.43		0.42	0.42	0.46	0.43–0.47	0.44
Index OE/BL	0.23		–	–	0.36–0.40		0.55	0.34	0.50	0.38–0.39	0.40
Index LSP/RSP	–		–	–	2.69–2.94		3.75	–	3.14	–	2.90

\*Probably a misprint



**Fig. 4** *Proyseria* sp. (male) from *Alcedo euryzona*, Malaysia. A, Anterior end, lateral (A1) and dorsoventral (A2) view; B, Posterior end, ventral view, note phasmids (arrows); C, Posterior end, sinistral view; D, Right spicule, dextral view; E, Postdeirid. Scale-bars are in micrometres

## Remarks

The male described above from *A. euryzona* corresponds in its morphology of the anterior body end, spicules and arrangement of the caudal papillae to other known males of *Proyseria*. In addition, by having a cuticular collar situated at the oesophageal region, this specimen resembles *P. alcedonis* (Puqin, Yanyin & Guocal, 1991) n. comb. (see Puqin et al., 1991). The latter was described from a single female collected from *A. atthis* in China and its male remains unknown. Therefore, a more precise comparison between these two samples is impossible. Nevertheless, the male individual described here complements our knowledge of the morphological diversity of the genus.

## Discussion

Until now, ten species have been assigned to the genus *Stegophorus* Wehr, 1934 (see below). With the exception of *Stegophorus alcedonis* Puqin, Yanyin & Guocal, 1991, a parasite of the common kingfisher *Alcedo atthis*, all other members of *Stegophorus* are parasites of seabirds of the orders Procellariiformes, Charadriiformes and Sphenisciformes. *Stegophorus alcedonis*, as described by Puqin et al. (1991), corresponds to the genus *Proyseria* with its collarette bearing cusps on the entire rim (including its anterior parts) and a vulva situated near the posterior extremity of the body. It differs from other *Stegophorus* spp. characterised by a collarette bearing cusps on the posterior part of their rim only and a vulva situated



near the mid-body. Therefore, we transfer this species to the genus *Proyseria* as *P. alcedonis* (Puqin, Yanyin & Guocal, 1991) n. comb.

Currently, the genus *Proyseria* consists of three nominal species parasitic in kingfishers: *P. decora* from *Alcedo atthis* recorded throughout the Palaearctic Region, *P. alcedonis* from *A. atthis* in China and *P. petterae* n. sp. from *Corythornis vintsioides* in Madagascar. The male specimen identified here as *Proyseria* sp. is probably conspecific with *P. alcedonis*, whose males remain unknown. In addition, the sample of *P. decora* from Vietnam, described by Ryzhikov & Khokhlova (1964), differs from the original description of the species (see comments above). The members of *Proyseria* are relatively uniform in the morphology of the left and right spicules, the arrangement of caudal papillae in males, the position of the vulva and the lengths of the muscular and glandular portions of the oesophagus (see Table 1). However, they can be easily distinguished by the morphology of the collarete and deirids as well as by the presence or absence of an additional cuticular collar. The small number of published records of *Proyseria* spp. as well as the low levels of intensity of infection (up to three specimens) characterise this acuariid genus as rare.

In view of the present morphological studies, we propose the following amended diagnosis of the genus *Proyseria*:

Small acuariid nematodes. Anterior end with two pseudolabia, each bearing single amphid and one pair of papillae. Anterior cuticular ornamentation in form of collarete, consisting of two lateral halves, with numerous teeth along their entire rims. Pseudolabia between two parts of collarete fused into single structure. Deirids large, with two or three cusps, situated anteriorly to nerve-ring. Excretory pore posterior to nerve-ring. Buccal cavity long, with conspicuous cross-striations. Muscular and glandular regions of oesophagus distinct. Phasmids subterminal. *Male*: with narrow caudal alae; precloacal pairs of papillae composed of single ventral sessile papilla and four pairs of papillae: pairs 1, 3 and 4 subventral and pedunculate, pair 2 sublateral; postcloacal papillae consisting of five pairs of pedunculate papillae and one pair of sessile papillae situated at the bases of pedunculate pairs of papillae; *area rugosa* absent, left spicule long, consisting of handle and blade; right spicule short and robust, armed by two prominent

cusps. *Female*: vulva posterior; *vagina vera* short, separated from short, muscular *vagina uterina* by well-developed circular musculature. Monodelphic. Under koilin lining of muscular stomach of the Alcedinidae (Coraciiformes). Type-species *P. decora* (Dujardin, 1845). Other species: *P. petterae* and *P. alcedonis*.

Wehr (1934) erected the genus *Stegophorus* to accommodate *Stegophorus stellaepolaris* (Parona, 1901). Later, Johnston & Mawson (1945) recognised *Paryseria* Johnston, 1937 as a junior synonym of *Stegophorus*. Skrjabin et al. (1965) reasonably corrected the generic definition specifying that the collarete of *Proyseria* is composed of two lateral parts instead of being a single structure surrounding the head region as stated by Wehr (1934).

The members of *Stegophorus* can be distinguished from those of *Proyseria* by their collarete bearing cusps on the posterior part of the rim, well-developed caudal alae in males, four pairs of subventral precloacal papillae, vulva situated at mid-body or slightly posteriorly, long ovejector and a didelphic female reproductive system.

Currently, the genus *Stegophorus* includes the following species:

- *Stegophorus stellaepolaris* (Parona, 1901) Wehr, 1934 [Syns *Histiocephalus stellaepolaris* Parona, 1901; *Streptocara stellaepolaris* (Parona, 1901) Skrjabin, 1916; *Yseria stellaepolaris* (Parona, 1901) Gedoelst, 1919] described from *Fulmarus glacialis* (L.) (type-host) in the Arctic (Parona, 1901). Subsequently, this species has been reported from diverse fish-eating seabirds of the orders Procellariiformes (Hydrobatidae, Procellariidae) and Charadriiformes (Alcidae, Laridae), mainly from the Arctic and sub-Arctic, e.g. *F. glacialis* from the North Sea and *Hydrobates pelagicus* (L.) in England (Baylis, 1928); *Uria lomvia* (L.) in the Greenland Sea and *F. glacialis* from the northern North Atlantic (Wehr, 1934); *F. glacialis* in Greenland (Baer, 1956); *F. glacialis* in the USA (Dunn, 1962); *Synthliboramphus antiquus* (Gmelin) in the USA (Schmidt, 1964); *Larus crassirostris* Vieillot and *U. lomvia* from the Peter the Great Gulf, Sea of Japan (Smetanina, 1981); *Stercorarius longicaudus* Vieillot and *Larus argentatus* Pontoppidan from the lower Yenisei River (Sergeeva, 1969); *Larus canus* L. and

- Hydrobates pelagicus* (L.) in Norway (Bakke & Barus, 1976a, b); *L. crassirostris* and *Uria aalge* (Pontoppidan) in the Rimsky-Korsakov Archipelago (Alekseev & Smetanina, 1968); *Alle alle* (L.), *Alca torda* L. and *U. aalge* near Newfoundland (Threlfall, 1971); *Puffinus gravis* (O'Reilly) in the USA (Foster et al., 1996); *Larus hyperboreus* Gunnerus in the Svalbard Archipelago (Sagerup et al., 2000); *U. aalge* and *U. lomvia* from the North Atlantic (Muzaffar, 2009).
- *Stegophorus adeliae* (Johnston, 1938) Johnston & Mawson, 1945 (Syn. *Paryseria adeliae* Johnston, 1938) from *Pygoscelis adeliae* (Hombron & Jacquinet) (Sphenisciformes: Spheniscidae) (type-host) in Commonwealth Bay, Antarctica (Johnston, 1938); *Pygoscelis papua* (J. R. Forster) on the Antarctic Peninsula (González-Acuña et al., 2013).
  - *Stegophorus diomedae* (Johnston & Mawson, 1942) Johnston & Mawson, 1945 from *Diomedea exulans* L. (Procellariiformes: Diomedidae) (type-host) and *Thalassarche melanophris* (Temminck) (= *Diomedea melanophris* Temminck) (Procellariiformes: Diomedidae), *Thalassarche chrysostoma* (J. R. Forster) (= *Diomedea chrysostoma* J. R. Forster) in Australia (Johnston & Mawson, 1942a, 1952); *T. melanophris* in Brazil (Rodrigues & Mendonça, 1967); *Puffinus gravis* (O'Reilly) in the USA (Foster et al., 1996).
  - *Stegophorus pachyptilae* (Johnston & Mawson, 1942) Johnston & Mawson, 1945 from *Pachyptila vittata* (G. Forster) (type-host) (Procellariiformes: Diomedidae) and *Pachyptila desolata* (Gmelin) in Australia (Johnston & Mawson, 1942a, b).
  - *Stegophorus macronectes* (Johnston & Mawson, 1942) Johnston & Mawson, 1945 from *Macronectes giganteus* (Gmelin) (Procellariiformes: Procellariidae) (type-host) and *Thalassarche chrysostoma* in Australia (Johnston & Mawson, 1942a); *M. giganteus*, *Stercorarius antarcticus lonnbergi* (Mathews) (= *Stercorarius skua loennbergi*) and *Chionis albus* (Gmelin) (Charadriiformes: Chionidae) on King George Island (Zdzitowiecki & Drózdź, 1980); *P. adeliae* in Atka Bay, Antarctica (Plötz, 1983); *Pygoscelis antarctica* (Forster) on Deception Island (Vidal et al., 2012); *P. papua* on King George Island (Diaz et al., 2013).
  - *Stegophorus paradeliae* Johnston & Mawson, 1945 from *Pygoscelis adeliae* (type-host) in Commonwealth Bay, Antarctica (Johnston & Mawson, 1945); *P. papua*, *Eudyptes chrysocome* (J. R. Forster) [= *Eudyptes cristatus* (Miller)] and *Eudyptes chrysolophus* (Brandt) on Heard Island, Australia (Mawson, 1953). Zdzitowiecki & Drózdź (1980) considered this species as a synonym of *S. macronectes*.
  - *Stegophorus heardi* Mawson, 1953 from *Oceanites oceanicus* (Kuhl) (Procellariiformes: Hydrobatidae) (type-host) and *Pelecanoides georgicus* Murphy & Harper (Procellariiformes: Hydrobatidae) on Heard Island (Australia) (Mawson, 1953).
  - *Stegophorus arctowski* Zdzitowiecki & Drózdź, 1980 from *S. antarcticus lonnbergi* (Mathews) [= *Stercorarius skua loennbergi* (Mathews)] (Charadriiformes: Stercorariidae) (type-host) and *M. giganteus* on King George Island (Zdzitowiecki & Drózdź, 1980).
  - *Stegophorus stercorarii* Leonov, Sergeeva & Tsimbalyuk, 1966 from *S. longicaudus* (Charadriiformes: Stercorariidae) (type-host), *Fratercula cirrhata* (Charadriiformes: Alcidae), *Fratercula cirrhata* (Pallas) and *Aethia cristatella* (Pallas) (Charadriiformes: Alcidae) on the Chukotka Peninsula, *Fulmarus glacialis* (L.) on the Commander Islands and *S. longicaudus* from the lower Yenisey River (Leonov et al., 1966); *Aethia pusilla* (Pallas) (Charadriiformes: Alcidae) in the Peter the Great Gulf, Sea of Japan (Smetanina, 1981) and in the Rimsky-Korsakov Archipelago (Alekseev & Smetanina, 1968); *S. longicaudus* and *Stercorarius pomarinus* Temminck from the lower Yenisey River (Sergeeva, 1969); *Synthliboramphus antiquus* (Gmelin) in Japan (Yokohata, 2003); *Puffinus tenuirostris* (Temminck) in Japan (Iwaki et al., 2012).

Despite of the numerous records of *Stegophorus* spp., the morphology of the majority of its species is known mainly from their brief original descriptions and further studies are needed.

More than 250 species classified in 45 genera within the family Acuariidae are known (Mutafchiev & Kinsella, 2012; Bain et al., 2014). Among these, the genera *Aviculariella* Wehr, 1931 (of the subfamily Acuariinae Railliet, Henry & Sisoff, 1912) and *Proyseria* Petter, 1959 (of the subfamily Seuratiinae Chitwood & Wehr, 1932), containing six and three species, respectively, are specific parasites of kingfishers (Mutafchiev et al., 2009; present study).

Kingfishers are also hosts of six out of the eight valid species of *Quasithelazia* Maplestone, 1932 (the subfamily Schistorophinae Travassos, 1918) (see Mutafchiev et al., 2014), one species of *Skrjabinoelava* Sobolev, 1964 (Acuariinae), one of *Ancyracanthopsis* Diesing, 1861 (Schistorophinae) and one of *Sobolevicephalus* Parukhin, 1964 (Schistorophinae) (see Wong & Anderson, 1983; Wong & Lankester, 1985a, b). In addition, two immature specimens of *Skrjabinocerca prima* Shikhobalova, 1930 (Acuariinae), usually parasitising chadriiform birds, were reported from *Halcyon pileata* (Boddaert) in the Rimsky-Korsakov Archipelago (Alekseev & Smetanina, 1968).

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