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Morphological and molecular characterization of *Prosthogonimus falconis* n. sp. (Trematoda; Prosthogonimidae), found in a peregrine falcon (*Falco peregrinus*) (Aves: Falconidae) in the United Arab Emirates

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Research Paper

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Abstract

At a routine health check of a female peregrine falcon, 23 trematodes preliminary identified as *Prosthogonimus* sp. were removed from the bursa of Fabricius. Based on morphological and molecular examination, a new species, *Prosthogonimus falconis*, was described. The pear-shaped flukes were 4.3–6.9 mm long, with greatest width posterior to testes. Tegumental spines measuring between 17 and 21 µm long covered the whole body. Length and width ratio of oral to ventral suckers were 1:1.3. Extracaecal, multifollicular vitelline glands commenced prior to acetabulum and terminated posterior to testes. Eggs in the distal uterus measured 21 × 12 µm. Molecular analysis of internal transcribed spacer 2, cytochrome *c* oxidase subunit 1 and NADH dehydrogenase subunit 1 gene regions revealed that the new species described here is phylogenetically closest to *Prosthogonimus cuneatus* and *Prosthogonimus pellucidus* clusters.

Introduction

Prosthogonimosis was an economically important parasitic disease in free-ranging chicken and has lost its significance under conditions of industrial poultry farming.

Rudolphi (1803) described *Fasciola ovata*, an egg-shaped, flat trematode of 3.3–4.5 × 2.2 mm in size with the acetabulum two times bigger than the oral sucker. The trematodes found in the bursa of Fabricius of a rook (*Corvus frugilegus*) were given to him by his friend, JCR Meyer. Later, Rudolphi (1809) described a similar trematode, *Distoma cuneatum*, in a great bustard (*Otis tarda*). *Distoma cuneatum* differed by a more pointed, cuneate shape, and eggs were concentrated posterior to ventral sucker. Rudolphi (1819) listed both species and added for the first species the common magpie (*Pica pica*), the northern shoveler (*Spatula clypeata*) and the Eurasian coot (*Fulica atra*) as further hosts.

Wedl (1858) gave more details on the morphology of a trematode that he found in the bursa of Fabricius of a common snipe (*Gallinago gallinago*), a common crane (*Grus grus*) and a Eurasian coot. He wrongly attributed this parasite to *Distoma ovatum*.

Another trematode with similar morphology was described in the oesophagus of a chicken (von Linstow, 1873; von Linstow found five specimens in the oesophagus, a rather unusual location – he pointed out that flukes with a related morphology (*D. ovatum*) were always reported from the bursa of Fabricius). Compared to previously described species, oral and ventral suckers had a similar size, intestinal caeca reached far behind ventral sucker, vitellaria terminated at posterior end of ventral sucker. Since uterine coils were less dense at the posterior end and the worm had a transparent appearance, the name *Distomum pellucidum* was chosen. Eggs and tegumental spines of *D. pellucidum* were longer than in previously known species of the extended genus *Prosthogonimus* created by Lühe (1899) for trematodes with a genital pore next to the left anterior end of the oral sucker and with parallel situated testes (in the same year, Looss (1899) proposed the genus *Prymnoprion*, but his paper was published three days later and for this reason *Prymnoprion* is treated as a junior synonym to *Prosthogonimus* (Stiles & Wardell, 1902)). Not mentioning *D. cuneatum*, the author recognized *D. ovatum* and *D. pellucidum* as valid species.

By re-examining materials of the Berlin collection, Braun (1902) concluded that *P. ovatus*, *P. pellucidus*, *P. japonicus* and *P. rarus* belong to the genus *Prosthogonimus* and restored the status of the fifth species, *P. cuneatus*.

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Already in the mid-1950s, the species inventory of the genus consisted of 23 species (Panin, 1957) and Skrjabin (1961) allocated all 37 known *Prosthogonimus* species to five subgenera.

Here, we present detailed morphological characteristics and phylogenetic analysis of a new *Prosthogonimus* species found in the bursa of Fabricius of a Peregrine falcon.

Materials and methods

During a routine clinical examination of a female peregrine falcon in January 2020, a fluke infection was detected in the bursa of Fabricius and a total of 23 moving, pink-coloured trematodes were removed and sent for species determination. Intact flukes were washed in phosphate-buffered saline, stained in an aquatic solution of carmine, dehydrated in rising alcohol concentrations and temporary slides embedded in glycerine were used to take measurements. For scanning electron microscopy (SEM), two flukes fixed in 70% ethanol were dehydrated by increasing concentrations of ethanol, critical-point dried using carbon dioxide (Leica EM CPD300; Leica, Wetzlar, Germany) and subsequently mounted on specimen stubs. Dried specimens were sputter-coated with a 10 nm layer of gold–palladium alloy (Polaron Sputter coater SC 7600; Emitech, Montigny-le-Bretonneux, France) before examination with a scanning electron microscope (Supra 40VP; Zeiss, Oberkochen, Germany).

For molecular analyses, total DNA was extracted from three fluke specimens using a DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) following the manufacturer's recommendation. We amplified the regions of nuclear (internal transcribed spacer 2 (ITS2)) as well as mitochondrial loci (cytochrome *c* oxidase subunit 1 (*cox*1) and NADH dehydrogenase subunit 1 (ND1), respectively), using the specific primers listed in Heneberg *et al.* (2015). Polymerase chain reaction (PCR) amplification was done in 25 µL reactions consisting of 12.5 µL of *Taq* PCR Master Mix (Qiagen), 0.4 µM of forward and reverse primers, 2 µL of DNA template and 8.5 µL of RNase-free water. Thermal protocol included initial polymerase activation at 95°C for 5 min followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 57°C (ITS2 and *cox*1) or 58°C (ND1) for 30 s, extension at 72°C for 1 min and final extension at 72°C for 7 min. After purification, amplicons were subjected to the Sanger sequencing in both directions using ABI 3130 DNA sequencer (Applied Biosystems, Waltham, USA). Sequence alignment and construction of phylogenetic trees were carried out using MEGA 7 software (Kumar *et al.*, 2016).

Nucleotide BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) analyses were done for sequences generated from the ITS2, *cox*1 and ND1 regions for preliminary identification. Program selection was optimized for the algorithm searching for somewhat similar sequences (blastn). Reference sequences were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/), and correlated with Heneberg *et al.* (2015). Datasets were constructed using MEGA 7 and aligned using the online version of MAFFT (version 7, https://mafft.cbrc.jp/alignment/server/) with the automated selection mode. The best model for maximum likelihood (ML) analyses for each gene region was selected, and the phylogenetic trees constructed using MEGA 7, with 1000 bootstrap replicas. The models used were as follows: ITS2 region – Kimura two-parameter model with gamma-distributed rates (K2 + G); *cox*1 and ND1 regions – Hasegawa–Kishino–Yano model with gamma-distributed rates with invariant sites (HKY + G + I). Trees were viewed and edited in MEGA 7 software.

One specimen of *Prosthogonimus* sp. is deposited in the Meguro Parasitological Museum with the registration number MPM Coll. No. 21737.

Results

Prosthogonimus falconis n. sp. (figs 1 and 2)

Type specimen. Holotype is deposited in the Meguro Parasitological Museum, Tokyo, Japan, with the registration number MPM Coll. No. 21737

Type host. Peregrine falcon, *Falco peregrinus* Tunstall, 1771 (Aves: Falconidae).

Site of infection. Bursa of Fabricius.

Intensity of infection. 23.

Type locality. Dubai, Dubai Emirate, United Arab Emirates (UAE) (25°08′28.18″N, 55°20′11.84″E).

Etymology. The species name is derived from the generic name of the host.

Light microscopy

Body flattened, 4.3–6.9 mm long, pear-shaped with greatest width posterior to testes, posterior end rounded (fig. 1 and table 1). Whole body covered with 17–21 µm-long triangle-shaped spines with a base 6–7 µm wide, sparse spination at posterior end. Subterminal oral sucker followed by small pharynx. Acetabulum in anterior half, slightly larger than oral sucker. Oesophagus 155 to 190 µm in length. Intestinal bifurcation in the first fifth of the body. Caeca terminate far posterior to testes in the last fifth of the body. Symmetrical unlobed testes intracaecal. Vasa deferentia unite between anterior rim of ventral sucker and intestinal bifurcation into a short common duct that pass into sausage shaped cirrus sac containing internal seminal vesicle. Common genital pore inconspicuous on left anterior rim of oral sucker. Ovary deeply lobed consisting of 9–11 lobes, posterior or partly dorsal to ventral sucker on opposite body half of genital pore. Seminal receptacle and Mehlis' gland postovarian. Extracaecal, multifollicular vitelline glands commence prior to acetabulum and terminate posterior to testes. Uterus with descending and ascending coils fill postacetabular space, partly overlapping testes and crossing distal intestinal caeca without forming loops in preacetabular space. Distal uterus as thin tube lateral to cirrus sac. Operculated eggs 21 × 12 µm.

SEM

Rim of the oral sucker with rosette-like structures, spineless. Rim of the ventral sucker with sparse spination. Body spines 10–11 µm long, spines at posterior body less dense. Egg shell covered with the net-like structure of irregular pore size (fig. 2a–e).

Molecular examination

Sequencing of PCR products generated ITS2 (585 bp), *cox*1 (438 bp) and ND1 (449 bp) sequences, which were deposited to GenBank under accession numbers OK044379, OK044305 and OK086769–OK086771, respectively. Three polymorphic sites with single nucleotide polymorphisms were detected within ND1 sequences of our three analysed fluke specimens. However, all mutations were silent, causing no change in the amino acid sequence.

Nucleotide BLAST analyses showed the highest similarity of our ITS2, *cox*1 and ND1 sequences to the respective sequences of

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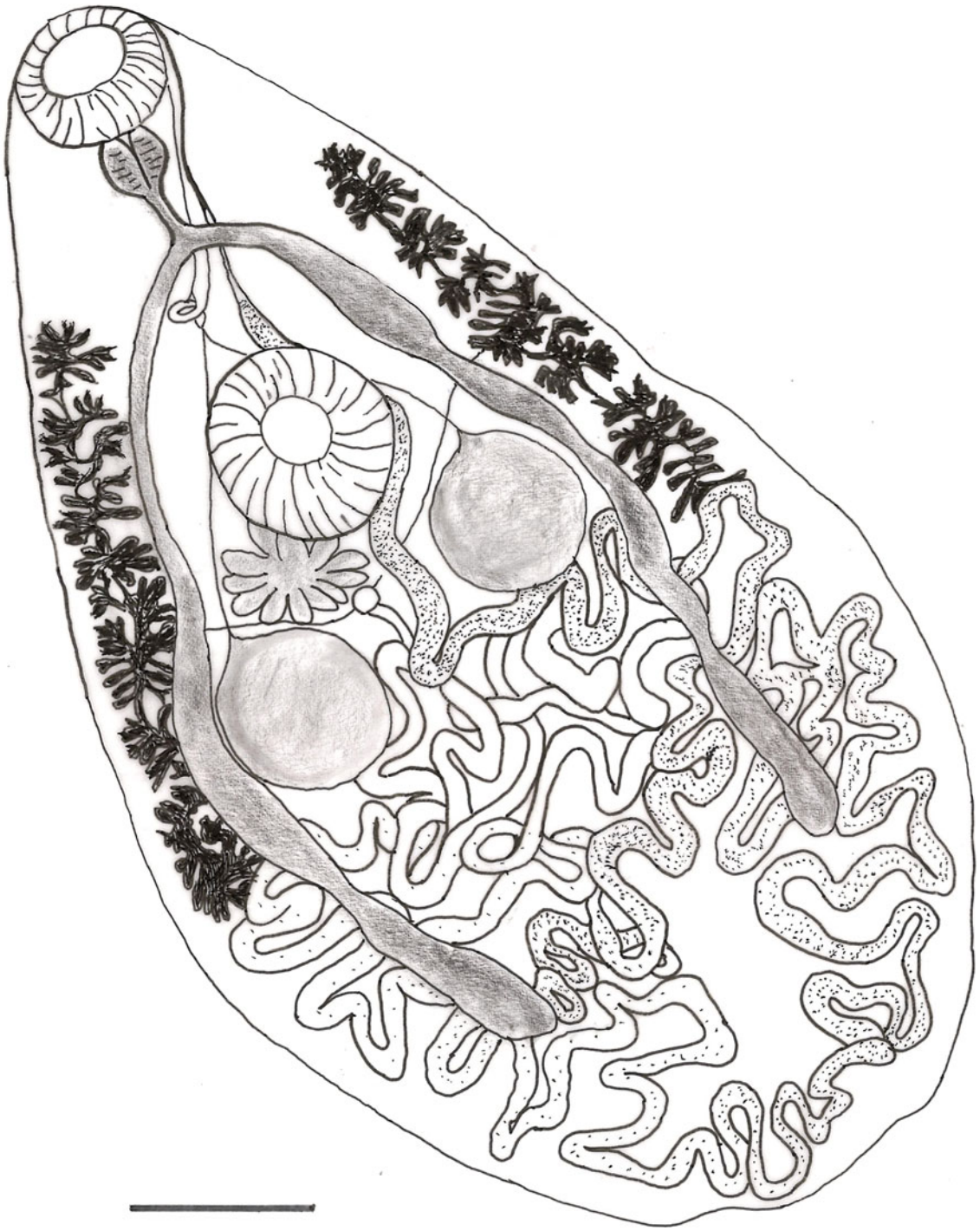

Fig. 1. *Prosthogonimus falconis*. Scale bar: 0.5 mm.

P. cuneatus (98.5%, 84.2% and 85.4%, respectively) from GenBank (accession numbers KP192725, KP192742, KP192757). In addition, ML analyses of individual sequences placed our fluke sample in a distinct clade, closely related to *P. cuneatus* and *P. pellucidus* clusters (fig. 3).

Discussion

Based on the morphology, it is difficult allocating our findings to any of the many described *Prosthogonimus* species. The paper of Heneberg *et al.* (2015) contains not only one of the most comprehensive morphological descriptions but also offers molecular data for four European *Prosthogonimus* species. In our case, *P. ovatus* can be excluded as the potential species since uterine coils in *P. ovatus* fill the entire space between vitelline glands, including the space dorsal to and in front of the ventral sucker; moreover, in *P. ovatus* body spination discontinues at the posterior edge of testes. Also, the suckers of *P. ovatus* are relatively small. Oral suckers in *P. ovatus*, *P. cuneatus* and *P. pellucidus* are roughly two times smaller than ventral suckers, while in *P. rarus* and in our material this relationship

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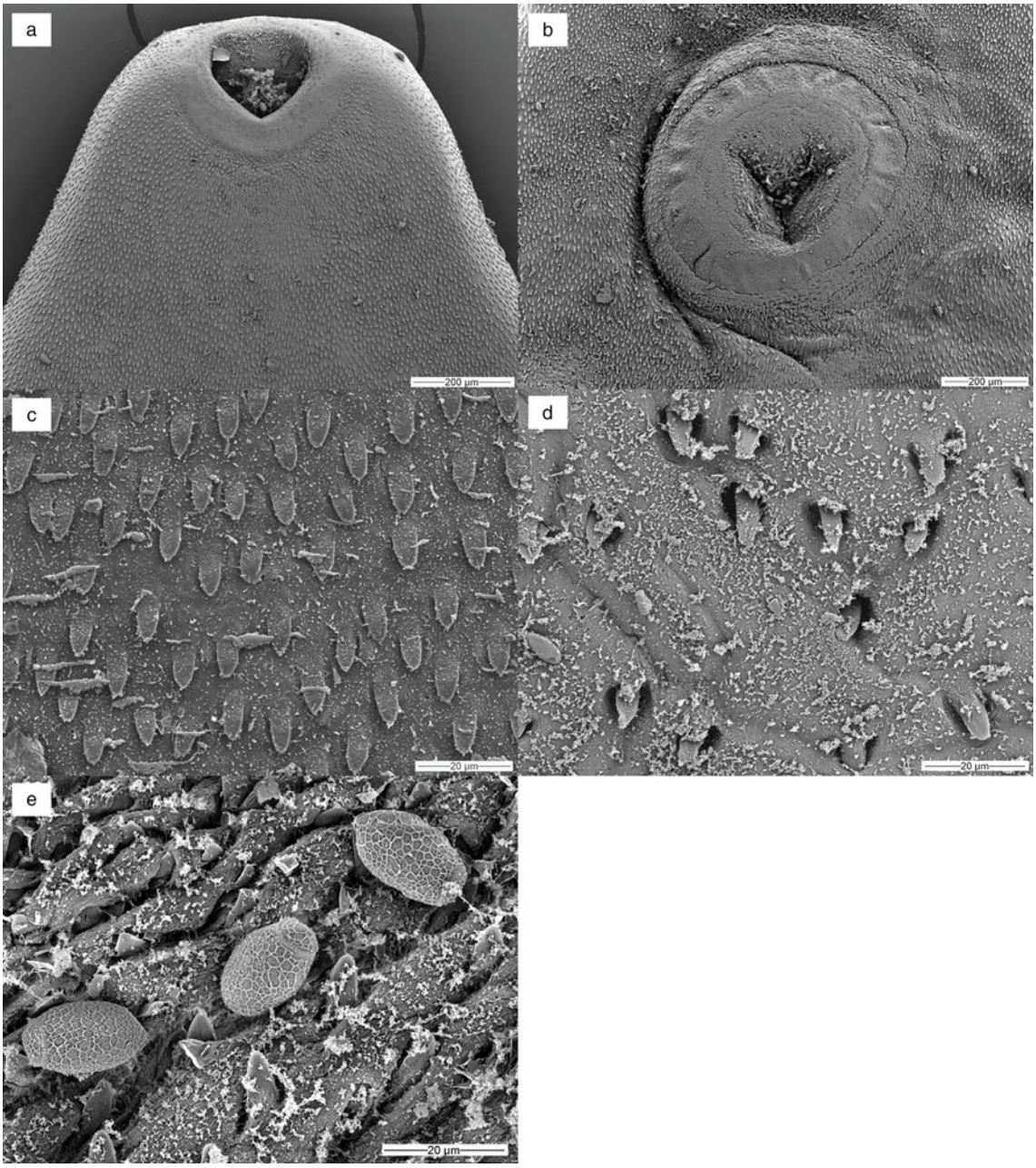

Fig. 2. SEM micrographs of *Prosthogonimus* sp. from the peregrine falcon: (a) anterior end with oral sucker and cirrus tip – the rim of the oral sucker with rosette-like structures is spineless; (b) ventral sucker; (c) body spines in anterior body part; (d) sparse spination at the posterior end; (e) eggs with net-like structure on the egg shell.

was 1:1.24 and 1:1.3, respectively. The maximum body width in *P. ovatus*, *P. cuneatus* and *P. pellucidus* is at the level of the testes, while in *P. rarus* and our material it is posterior to the testes. *Prosthogonimus rarus* differs by long intestinal caeca, intracaecal uterine loops and broad vitelline glands that partly overlap the caeca. Our *Prosthogonimus* specimens from a falcon reveal tegumental spines also on distal body, although spination was less dense and spines were 17–21 µm long by light microscopy, comparable to those of *P. rarus* (17–24 µm). Measurements on the SEM image revealed shorter lengths, but this is most likely the case because the bases of the spines are deeply embedded in the tegument covering parts of the entire surface. The SEM image of *Prosthogonimus* eggs showed a net-like structure on the shell similar to other small trematode eggs (Shin *et al.*, 2009; Lee *et al.*, 2012). Eggs in the distal uterus in our material measured only 23 × 14 µm, closest to the eggs from *P. cuneatus* (26 × 14 µm), and they were considerably smaller than those of other species. With regards to other European *Prosthogonimus* species, our material can be distinguished from *Prosthogonimus longusmorbificans*, which has a large body length of 14–16 mm, nearly equal dimension of suckers and short vitellaria, from *Prosthogonimus macrorchis*, which has testes larger than ventral sucker and very short vitellaria, and from *Prosthogonimus limani* with a differently structured uterus.

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Table 1. Morphology of four *Prosthogonimus* species according to Heneberg *et al*. (2015) and own data.

Parameter	*P. cuneatus* (15/5)[a]	*P. pellucidus* (11/1)	*P. ovatus* (30/3)	*P. rarus* (15/2)	*P. falconis* n. sp. (13/1)
Body length (mm)	4.6 (4.1;5.10)	5.1 (3.6;6.2)	4.1 (3.3;5.6)	5.1 (4;6.8)	5.6 (4.3;6.9)
Body width (mm)	2.6 (1.7;3.7)	2.3 (1.8;3.4)	1.9 (1.5;2.2)	3.3 (2.4;4.1)	3.4 (2.8;3.9)
Oral sucker length[b]	243 (238;534)	311 (255;402)	184 (122;340)	432 (290;524)	640 (544;760)
Oral sucker width	339 (267;598)	292 (174;340)	184 (139;340)	453 (290;644)	653 (508;717)
Pharynx length	168 (128;276)	147 (81;186)	124 (99;202)	177 (116;230)	197 (160;230)
Pharynx width	179 (133;244)	151 (110;202)	127 (93;193)	228 (162;294)	224 (140;300)
Ventral sucker length	646 (493;920)	614 (467;763)	400 (248;460)	538 (414;736)	852 (707;1000)
Ventral sucker width	667 (522;929)	575 (460;690)	399 (319;460)	556 (435;690)	844 (770;903)
Ventral: oral sucker length ratio	1.96 (1.21;3.23)	1.96 (1.21;2.54)	2.25 (1.23;3.09)	1.24 (0.96;1.9)	1.3 (1.2;1.7)
Ventral: oral sucker width ratio	2.02 (1.18;3.33)	2.02 (1.59;3.39)	2.24 (1.24;3.17)	1.24 (1.11;1.9)	1.3 (1.1;1.7)
Ovary length	603 (319;1311)	441 (304;626)	553 (386;736)	603 (319;1311)	585 (503;673)
Ovary width	604 (248;1118)	347 (276;690)	548 (184;920)	604 (248;1148)	694 (667;715)
Left vitellarium length	1749 (1286;2414)	1546 (942;2200)	Not mentioned	1567 (1143;2143)	1977 (1440;3230)
Right vitellarium length	1690 (1229;2860)	1597 (857;2286)	Not mentioned	1543 (827;2057)	2186 (1640;2430)
Left testes length	594 (478;810)	478 (386;626)	748 (348;1118)	604 (408;856)	813 (642;1017)
Left testes width	468 (267;454)	322 (230;478)	440 (174;745)	119 (276;644)	667 (480;800)
Right testes length	575 (478;775)	476 (340;616)	732 (290;1088)	595 (350;828)	862 610;1070)
Right testes width	437 (232;662)	329 (121;460)	438 (174;745)	415 (276;570)	640 (530;770)
Egg length	29 (26;34)	26 (24;60)	29 (29;34)	29 (26;31)	21 (19;23)
Egg width	16 (14;17)	14 (12;14)	14 (14;17)	14 (12;17)	12 (11;14)
Spine length	32 (22;36)	12	12 (10;14)		17–21
Spination	Except post part	Except post part	Up to posterior to testes	Whole body	Whole body
Maximum body width	At testes	At testes	At testes	Posterior to testes	Posterior to testes

[a]Numbers in the parentheses represent the number of examined specimens/number of examined hosts
[b]All measurements are in μm except for body length and body width, which are given in mm

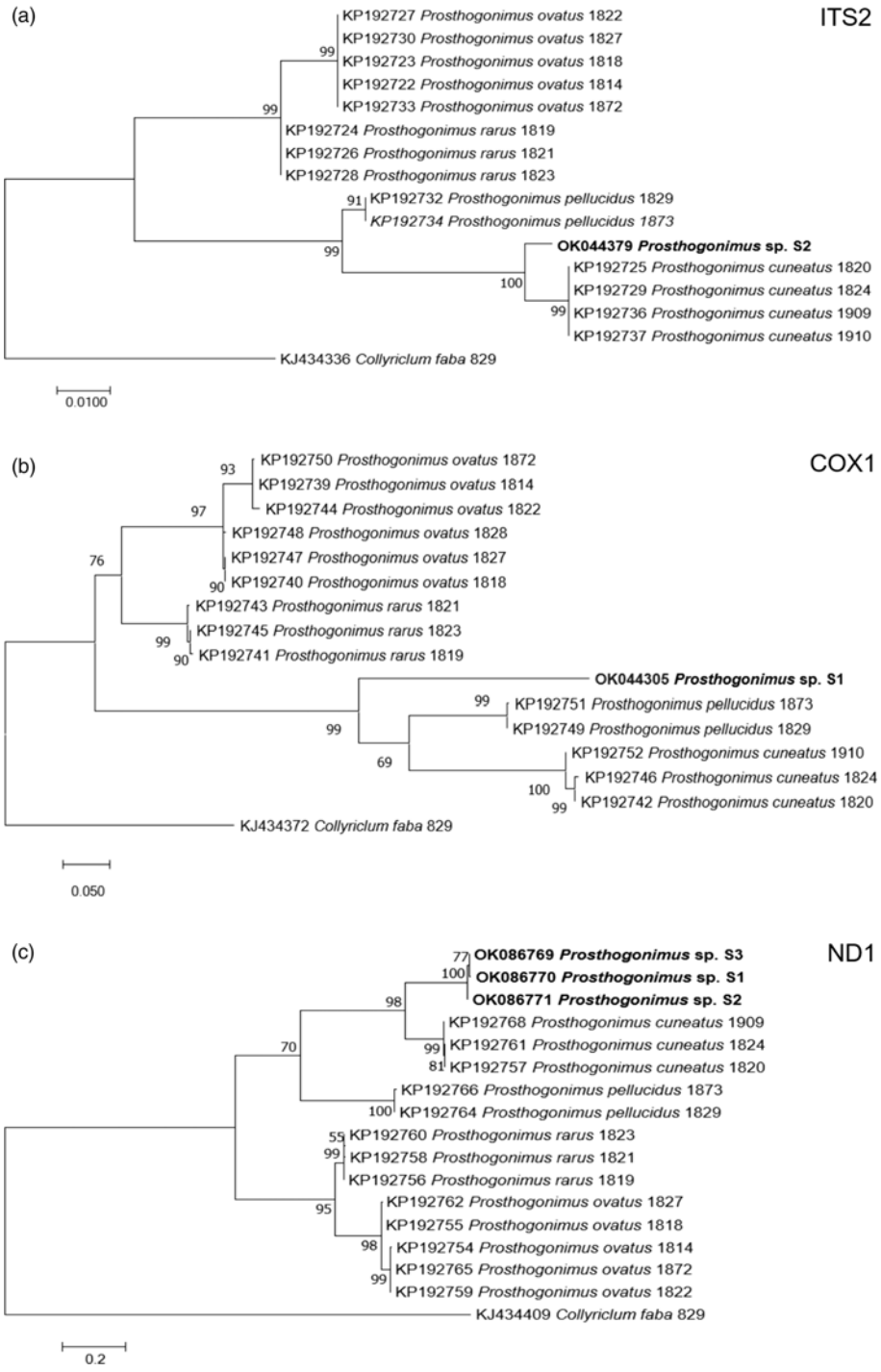

Fig. 3. ML analysis of *Prosthogonimus* spp. sequences from GenBank. (a) ITS2; (b) *cox*1; (c) ND1. Sequences generated from the specimens analysed in our study are bolded. The bar represents percentage of genetic variation.

According to Skrjabin's (1961) division, *F. falconis* would belong to the subgenus *Macrogenotrema* Skrjanin & Basakov, 1925 in which *P. cuneatus* was assigned as type species. This subgenus combines species with well-developed reproductive organs and a uterus that forms lopes only posterior to the ventral sucker and these lopes overlay blind-ending caeca. Five species – namely, *Prosthogonimus hyperabadensis* Jaiswal, 1957, *Prosthogonimus indicus* Srivastava, 1938, *Prosthogonimus ketupi* Jaiswal, 1957, *Prosthogonimus macroacetabulus* Chauhan, 1940 and *Prosthogonimus singhi* Jaiswal, 1957 – were described from India as a country relatively close to the UAE. From other countries close to the UAE, *P. cuneatus* was found in *Falco tinnunculus* (Mohammed, 1999) and recently, Saeed *et al.* (2019) reported a new species, *Prosthogonimus jonesae* found in *Vanellus indicus* in Pakistan. Sadaf *et al.* (2021) claimed that they found eggs of *P. ovatus* and *P. macrorchis* in faecal smears of domestic birds in Punjab, Pakistan in a prevalence of 12.1% and 9.1%, respectively. A curious finding of *P. macrorchis* in the albumen of an egg was described by Naem & Golpayegani (2003) in Iran. The other species reported from Iran was *P. ovatus*, found in *P. Pica* in a prevalence of 11.3% (Halajian *et al.*, 2011).

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Table 2. Morphology of *Prosthogonimus* species described from India, Pakistan and Kazakhstan in comparison to *Prosthogonimus falconis* (measurements are in mm unless stated otherwise).

Species	*P. hyperabadensis*	*P. indicus*	*P. ketupi*	*P. macroacetabulus*	*P. singhi*	*P. jonesae*	*P. putschkovski*	*P. falconis*
Host	*Bubulcus ibis*	*Gallus domesticus*	*Ketupa ceylonensis*	*Passer domesticus*	*Ardeola grayi*	*Vanellus indicus*	*Platalea leucorodia*	*Falco peregrinus*
Country of origin	India	India	India	India	India	Pakistan	Kazakhstan	UAE
Body length	6.3–7.8	4.8–8.0	10–11.7	3.0	4.8–5.2	4.1–4.8	7	5.6
Body width	2.6	2.0–2.8	4.0–4.3	1.0	1.6–2.0	2.3–3.5	5	3.4
Oral sucker length	0.47	0.18–0.32	0.8–0.9	0.3	0.5	0.3	0.8	0.64
Pharynx length	0.23	0.2	0.26	0.11	0.15	0.2	0.3	0.2
Oesophagus length	0.3	0.32–0.38	0.95	0.07	0.27		0.38	0.16–0.19
Ventral sucker length	0.97–1.1	0.66–1.2	1.3	0.64	0.9	0.8	1.1–1.2	0.85
Oral: ventral sucker	1:2.1	1:3.1	1:1.4	1:2.1	1:1.8	1:2.7	1:1.25	1:1.32
Ovary	0.86 × 0.8	0.4–0.7 × 0.6–1	1.3–1.7 × 1.0	0.3 × 0.35	0.48 × 0.74	0.4 × 0.4	Not reported	0.6 × 0.7
Testes shape	Oval	Round	Oval	Round	Long oval	Oval	Round	Round to oval
Testes length	0.76–0.97	0.4–0.7	1.6–1.8	0.3	0.8	0.55	1.1–1.4	0.8
Testes width	0.47–0.57	0.4–0.78	1.0	0.4	0.4	0.44	1.1–1.4	0.65
Eggs (μm)	22–28 × 12–16	19–21 × 11–15	32 × 15	18–26 × 5–12	25–31 × 13–16	15–20 × 10	26 × 14	21 × 12
Body supination (μm)	Present	15	Not reported	9–12	yes	Not reported	20–33	17–21

All the named species here are morphologically different from *P. falconis* (table 2).

Prosthogonimus hyperabadensis, *P. indicus* and *P. macrorchis* differ as they have an elongated body size. The dimensions of *P. ketupi* are considerably larger, those of *P. macrorchis* smaller than those of *P. falconis*. Tegumental spines of *P. indicus* and *P. macorchis* are shorter and not reported for *P. jonesae*. In *P. hyperabadensis*, *P. indicus*, *P. macrorchis* and *P. jonesae* relation of ventral to oral suckers are >1:2 and eggs of *P. ketupi*, *P. singhi* and *Prosthogonimus putschkovski* are larger than those of *F. falconis*.

Our newly determined gene sequences showed the highest similarity to those of *P. cuneatus*. However, percent identity between compared sequences ranged from 84.2% to 98.5%, overcoming intraspecies variation within *P. cuneatus* and suggesting that our sample belongs to a different species. In addition, phylogenetic dendrograms that were constructed according to ITS2, *cox*1 and ND1 sequences, designated our sample as a separate species. However, we cannot be sure if it represents a new *Prosthogonimus* species or one of the existing species that was described only based on morphological criteria, but without molecular confirmation. Therefore, future studies on *Prosthogonimus* spp. should also include sequencing data in order to corroborate the validity of morphological identification and avoid any bias in species identification.

Since members of the genus *Prosthogonimus* have a semi-aquatic life cycle with prosobranch snails as first and dragon- and damselflies as second intermediate hosts, prosthogonimosis was more often diagnosed in water birds with water as natural habitat (Anseriformes, Ralliformes, Charadriformes, Lariformes), but also in birds of the orders Passerifomes and Galliformes. Only very few infections of birds of prey have been recorded so far from Poland (*Falco subbuteo* by von Siebold, 1836; *Accipiter nissus* and *F. subbuteo* by Sulgostowska & Czaplinska, 1987), Russia (*F. tinnunculus* and *Falco vespertinus* by Skrjabin & Baskakow, 1925), Iraq (*F. tinnunculus* Moammed, 1999), the Netherlands (*F. subbuteo* by Borgsteede *et al.*, 2003) and Czech Republic (*F. subbuteo* by Heneberg *et al.*, 2015).

Unfortunately, neither information on the origin nor on the history of the infected peregrine falcon could be obtained. Birds become infected by ingesting dragonflies or damselflies or their larval stages. According to a survey by Lambret *et al.* (2017), some of the genera of damselflies, hawkers and skimmers that can act as second intermediate hosts are present in the UAE.

As far as it is known, prosobranch snails of the genus *Bithynia* (*Bithynia tentaculta* and *Bithynia leachi* complex) are known as first intermediate hosts. These snails are quite common in the northern Palearctic, and representatives of the genus *Bithynia* occur in central Asian republics, in Iran and India, but they are absent in the UAE (Feulner & Green, 1999).

Since hunting with falcons is restricted in the UAE, many falconers go on hunting trips to Pakistan, Iran, Afghanistan and central Asian republics or to Morocco where they can find bigger concentrations of bustards, and it is quite possible that the infection was acquired in one of these countries. Maralbayeva & Akhmetov *et al.* (2019) examined birds in Kazakhstan and detected only two members of the genus *Prosthogonimus* – *P. rarus* and *P. cuneatus* – while Khasanova (2019) reported only *P. ovatus* for Uzbekistan.

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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.

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