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Gastrointestinal helminths of the Australasian harrier (*Circus approximans* Peale, 1848) in New Zealand, and description of a new species of nematode, *Procyrnea fraseri* n. sp. (Habronematidae)

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Research Paper

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Abstract

The Australasian harrier *Circus approximans*, a native of Australia, New Zealand and the South Pacific, is an opportunistic hunter of small prey, although a large part of its diet consists of carrion, mainly from roadkill. Besides a record of a single, unnamed species of capillariid nematode there have been no investigations into the parasites of Australasian harriers in New Zealand. In this study, a helminthological survey of sixty-five deceased harriers from southern New Zealand uncovered a gastrointestinal helminth fauna consisting of six parasite species. *Porrocaecum circinum* (Nematoda) was previously described only from fragmented females, and a redescription is presented here. *Procyrnea fraseri* n. sp. (Nematoda) is described, and distinguished from its congeners by its slender body shape and shorter spicules. *Strigea falconis* (Trematoda) is reported for the first time in New Zealand. *Cladotaenia anomalis* (Cestoda) and *Polymorphus circi* (Acanthocephala) were previously described as new species elsewhere. An unnamed species of capillariid appears to be mainly confined to North Island and is rare in South Island. Prevalence and intensity metrics are given, and DNA sequences provided to accompany new re/descriptions. Potential intermediate hosts are discussed, and the origins of the helminths and their potential for pathogenicity are considered.

Introduction

The Australasian harrier *Circus approximans* Peale (Accipitriformes: Accipitridae), also known as swamp harrier, harrier hawk or kāhu, is native to Australia, New Zealand and some islands in the South Pacific (Debus & Kirwan 2020). It is thought to have colonised New Zealand from Australia subsequent to human arrival and probably became established following the habitat disturbances associated with humans in the last 800 years (Holdaway & Worthy 1997). This species is an opportunistic hunter of live prey such as small birds, mammals and invertebrates, and also a scavenger, with carrion making up a major component of the diet (Baker-Gabb 1981; Robertson 1980). In New Zealand, harriers hunt mainly in open habitats and the ready availability of road-kill carcasses has seen the harrier rise to healthy population numbers (Eakle 2008). Although the conservation status of harriers is 'Not Threatened' according to the New Zealand Threat Classification System (Robertson *et al.* 2021), the bird is considered a taonga ("treasured") species by Māori and is partially protected by law (Wildlife (Australasian Harrier) Notice 2012). Potentially due to their 'road-kill' feeding habits, many harriers are themselves often victims of roadkill or injury (Sadleir & Linklater 2016) meaning a large number of deceased individuals pass through wildlife centers throughout New Zealand. Despite this, there have been few studies on the parasitic helminths of Australasian harriers in New Zealand, and only one parasite species reported so far (*Capillaria* sp. in Alley *et al.* (2004) and French *et al.* (2020)). As far as we can ascertain there are no parasite records for Australasian harriers from any other part of their range.

Research on gastrointestinal helminths can offer valuable insight into aspects of host health, evolution and ecology, and the relative health of the wider ecosystem (Marcogliese 2005; Bennett *et al.* 2023). For instance, changes in a predator's diet associated with climate change or human activities that threaten prey populations can be reflected in alterations to helminth compositions (Lozano 1991). Before any assessment of change can be performed however, it is crucial that basic data of parasite-host associations is obtained. Unfortunately, baseline data on helminth assemblages within specific host species are often incomplete, especially in New Zealand (Mckenna 2010; Bennett *et al.* 2022). An opportunity to access a relatively large number of deceased harriers from the southern half of South Island between 2017 and 2023 has led to the characterization of parasitic helminths infecting Australasian harriers in New Zealand. Here we present an

annotated list of those helminths found in the harriers examined, including a description of a new species of *Procyrnea,* redescription of *Porrocaecum circinum* Johnston & Mawson, 1941 and the first report of *Strigea falconis* Szidat, 1928 from New Zealand. We note the presence of an unknown capillariid nematode. We discuss potential intermediate hosts, and consider the origins of the helminths and their potential for pathogenicity. Two additional species new to science, a cestode and an acanthocephalan, are reported here but have recently been described separately (Presswell and Bennett (2023a, 2023b)).

Materials and methods

Harrier collection and processing

A total of 65 harriers was examined for parasitic helminths. Of those, 46 were from Otago, donated by the Dunedin Wildlife Hospital or collected as roadkill by the first author between 2017 and 2022, and 19 individuals were from Canterbury, donated by The New Zealand Raptor Trust between 2022 and 2023. Birds were frozen upon collection and defrosted prior to dissection. Helminths were collected and preserved in 70% ethanol for whole-mount, 96% ethanol for genetic analyses and 4% buffered formalin for later SEM imaging.

Morphological data

Nematode specimens were cleared in lactophenol and acanthocephalan specimens were cleared in beechwood creosote as temporary mounts for light microscopy. Cestode and trematode specimens were stained using acetic acid iron carmine, dehydrated in an ethanol series, cleared in clove oil and permanently mounted with Canada balsam. Measurements were made using ImageJ software (Wayne Rasband, NIH, USA) from photographs taken on an Olympus BX51 compound microscope mounted with DP25 camera attachment (Olympus, Tokyo). All measurements are in micrometres unless otherwise indicated, and in descriptions are given as range, followed by mean in parentheses, where numbers permit. Drawings were made from photographic series.

Specimens chosen for scanning electron microscopy (SEM) were transferred to 2.5 % gluteraldehyde in 0.1 M phosphate buffer, post-fixed in 1% osmium tetroxide and dehydrated through a gradient ethanol series, critical-point dried in a CPD030 BalTec critical-point dryer (BalTec AG, Balzers, Liechtenstein) using carbon dioxide, mounted on aluminium stubs, and sputter coated with gold/palladium (60:40) to a thickness of 10 nm in an Emitech K575X Peltier-cooled high-resolution sputter coater (EM Technologies, Ashford, Kent, UK). The specimens were viewed with a JEOL 6700 F field emission scanning electron microscope (JEOL Ltd., Tokyo, Japan) or Zeiss Sigma VP variable-pressure scanning electron microscope (Carl Zeiss Inc., Oberkocken, Germany) at the Otago Centre for Electron Microscopy (OCEM, University of Otago, New Zealand).

Parasites were morphologically identified to the lowest taxonomic level possible. Taxa unfamiliar to the authors were identified using morphological keys such as Khalil *et al.* (1994), Gibbons (2010), Gibson *et al.* (2002), Bray *et al.* (2008), and original species descriptions.

Molecular data and analyses

Specimens of each species were chosen for DNA sequencing. Genomic DNA was extracted using the DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. For the strigeid trematode, a partial fragment of 28S ribosomal RNA gene was amplified using T16 and T30 primers (Harper & Saunders, 2001) and conditions of 94°C for 5min, 38 cycles of 94°C for 30sec, 45°C for 30sec and 72°C for 2min, and 72°C for 7min. Additionally, *cox1* and nad1 were amplified using primers JB3 (Bowles *et al.* 1992) and trem.cox.rrnl (Králová-Hromadová *et al.* 2001), and JB11 (Morgan & Blair 1998) and NDJ2a (Kostadinova *et al.* 2003) respectively. The *cox*1 conditions followed 95°C for 2min, 40 cycles of 95°C for 30sec, 48°C for 40sec and 72°C for 1min, and 72°C for 10min, and the nad1 conditions followed that of Georgieva *et al.* (2013). For nematodes, either the 18S and/or internal transcribed spacer (ITS1) genes were targeted using Nem18SF and Nem18SR (Wood *et al.* 2013) and SS1 and NC13R (Shamsi *et al.* 2008) primers respectively. The 28S PCR conditions consisted of 94°C for 5min, 38 cycles of 94°C for 30sec, 52°C for 30sec and 72°C for 1min, and 72°C for 10min. The 18S and ITS PCR conditions followed Wood *et al.* (2013) and Shamsi *et al.* (2008). All PCR products were cleaned using EXOSAP-TMTM Express PCR Product Cleanup Reagent (USB Corporation, Cleveland, OH, USA), following manufacturer's instructions. Sanger sequencing by capillary electrophoresis was performed by the Genetic Analysis Service, Department of Anatomy, University of Otago (Dunedin, New Zealand).

Sequences were imported to Geneious Prime®v1.2, trimmed using the trim function with default parameters, and manually edited for incorrect or ambiguous base calls. Sequences were used in BLASTn searches on GenBank® to establish a preliminary identification. Newly generated sequences are listed in Table 1, with their associated GenBank accession numbers. Some sequences were further explored with closely related sequences on GenBank following the BLASTn searches using Bayesian inference. In total, three phylogenetic analyses were performed: ITS gene with species of Genus *Porrocaecum*, 18S gene involving species within Spiruromorpha and *cox*1 gene for representatives within Family Strigeidae. The program JModelTest v2.1.6 (Posada 2008) was used to estimate the model of evolution for the three alignments, restricted

Table 1. Newly generated sequences of parasites infecting Australasian harrier in the South Island of New Zealand, and including genes targeted, isolate ID and GenBank accession numbers

		GenBank Accession Number				
Parasite species	Isolate ID	18S	ITS	28S	*cox*1	NAD
Porracaecum circinum	har37nem1	OR820168	OR827722			
Procyrnea fraseri n. sp.	har15nem1	OR820169				
Strigea falconis	har32tre1			OR827721	OR826952	OR842556
	har9tre1			OR827720		

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to three substitution models compatible with MrBayes. The models selected were HYK+G for *Porrocaecum* ITS alignment, GTR+I for Spiruromorpha 18S alignment and HYK+I+G for the Strigeidae *cox*1 alignment. Bayesian inference was conducted for each alignment using the online interface: Cyberinfrastructure for Phylogenetic Research Science Gateway (CIPRES) (Miller *et al.* 2010). The analyses performed had random starting trees for two runs (each with one cold and three heated chains), employing a Markov Chain Monte Carlo approach for sampling the joint posterior probability distribution across 10,000,000 generations. The resulting trees were summarized in a 50% majority-rule consensus tree with clade credibility support values (Bayesian Posterior Probability, BPP) and branch length information. Trees were visualised in FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and edited in Inkscape v1.1 (downloaded from https://inkscape.org). A BPP higher than 0.8 was considered moderately supported and greater than 0.95 was considered high nodal support. Uncorrected pairwise genetic distances were estimated in MEGA v.11.0.13 (Tamura *et al.* 2021).

Results

In total, 6 helminth parasite species were recovered from 65 harrier specimens: 2 nematodes, 1 trematode, 1 acanthocephalan and 1 cestode, along with remains of a capillariid nematode. Eighty percent of individuals (52/65) were infected with at least one species of gastrointestinal helminth. The cestode, *Cladotaenia anomalis* Presswell & Bennett, 2023 was the most prevalent species, occurring in over half of the birds examined. The parasite with the highest mean intensity was the acanthocephalan, *Polymorphus circi* Presswell & Bennett, 2023, although none of the helminths was found in very large numbers (infection data are summarised in Table 2). Below we provide a taxonomic redescription of the nematode *Porrocaecum circinum,* a description of new species *Procyrnea fraseri* n. sp., a brief description of the trematode *Strigea falconis*, and brief remarks for *Cladotaenia anomalis*, *Polymorphus circi*, and the unidentified capillariid nematode.

Table 2. Prevalence and intensity data of helminths found in Australasian harriers (n = 65), from Otago and Canterbury, South Island, New Zealand

	prevalence: number of birds (%)	Intensity range (average)
Nematoda		
Porrocaecum circinum	26 (40%)	1-15 (2.6)
Procyrnea fraseri n. sp.	12 (18%)	1-30 (5.4)
Trematoda		
Strigea falconis	4 (6%)	1-15 (5.8)
Cestoda		
Cladotaenia anomalis	37 (57%)	*1-15+
Acanthocephala		
Polymorphus circi	4 (6%)	1-40 (12.5)

*It is not possible to precisely count the number of cestodes as most were in many pieces.

NEMATODA Cobb, 1932
Ascaridida Skrjabin et Schulz, 1940
Ascaridoidea Baird, 1853
Ascarididae Baird, 1853
***Porrocaecum* Railliet & Henry, 1912**
***Porrocaecum circinum* Johnston & Mawson, 1941 [Figure 1–2; Figure 6a]**

Specimens of a *Porrocaecum* species were found in 40% of harriers examined, identifiable by their prominent lips with dentigerous ridges, presence of interlabia, oesophagus with oblong ventriculus but without ventricular appendix, and wide intestinal caecum (Hartwich 2009). The worms were found in the intestine, and infections included immature and mature adults, with a large size range from 23mm to 125mm. Sexual size dimorphism was evident and females were larger than males. Based on a literature search the specimens were identified as probable examples of *P. circinum*, a species described from a related harrier (*Circus assimilis* Jardine & Selby) in Australia. The original description included only fragmented females, so we present below a more complete redescription of females, and the first description of males.

Redescription:

General. Large sized, whitish or partially pink nematodes with transversely striated cuticle. Maximum width at about mid-body. Lips well developed, approximately hexagonal, narrower at base than anterior margin. Dorsal lip with one pair of large double papillae, subventral lips each with one double papilla, one small papilla and amphid (Figure 1a–c; Figure 2a–b). Anterior and lateral margins of lips armed with about 80–100 acuminate denticles; dentigerous ridge continuing along edge to below lateral wing-like expansion on each side of lip, and extending nearly to its base. Interlabia small, triangular, about 32–44% of lip length. Labial pulp subdivided distally into two lobes, each further subdivided into a pair of finger-like projections (Figure 2c). Lateral alae narrow, starting near base of subventral lips, extending almost to tail in both sexes. Cervical papillae not observed. Oesophagus muscular, more or less cylindrical. Ventriculus distinctly longer than wide, bullet-shaped with anterior end flattened and slightly wider that oesophagus (Figure 1c). Intestinal caecum long, 53–66% of oesophageal length. Nerve-ring at about 14–19% of oesophageal length. Excretory pore just posterior to nerve-ring. Tail of both sexes conical, with a very small mucron, 12–24µm long.

Male (based on 3 mature, 2 immature specimens, 1 SEM specimen and several part specimens): Body length (BL) 25–73mm; maximum width 450–1013. Lips 108–193 long. Interlabia 56–85 long. Oesophagus 2.3–4.2 mm long, representing 5.8–7.6% of body length. Nerve-ring and excretory pore 432–690 and 584–837 respectively, from anterior extremity. Ventriculus 254–677 long. Intestinal caecum 1.39–2.50 long, representing 59–66 % of oesophageal length. Posterior end of body distinctly curved ventrally; tail 245–363 long with distinct constriction posterior to cloaca. Spicules alate, almost equal in length, ala extending beyond distal end and sub-rounded, 581–984 long, representing 1.3–1.93 % of BL (Figure 1f). Gubernaculum absent. Caudal papillae 26–27 pairs in total: 21–22 pairs precloacal, 1 pair double paracloacal (slightly posterior to cloaca) and 4 pairs postcloacal (proximal pair lateroventral, second pair ventral, 3rd and 4th pairs in a rough row 2 lateroventral and 2 ventral) (Figure 2d). Single medio-ventral precloacal papilla absent. Internal opening of cloaca highly rugose with distinct band on anterior lip. Phasmids very small, located lateral to second row of papillae.

Female (based on 4 mature, 6 immature, 2 SEM specimens and several part specimens): Body length 26–125 mm; maximum width

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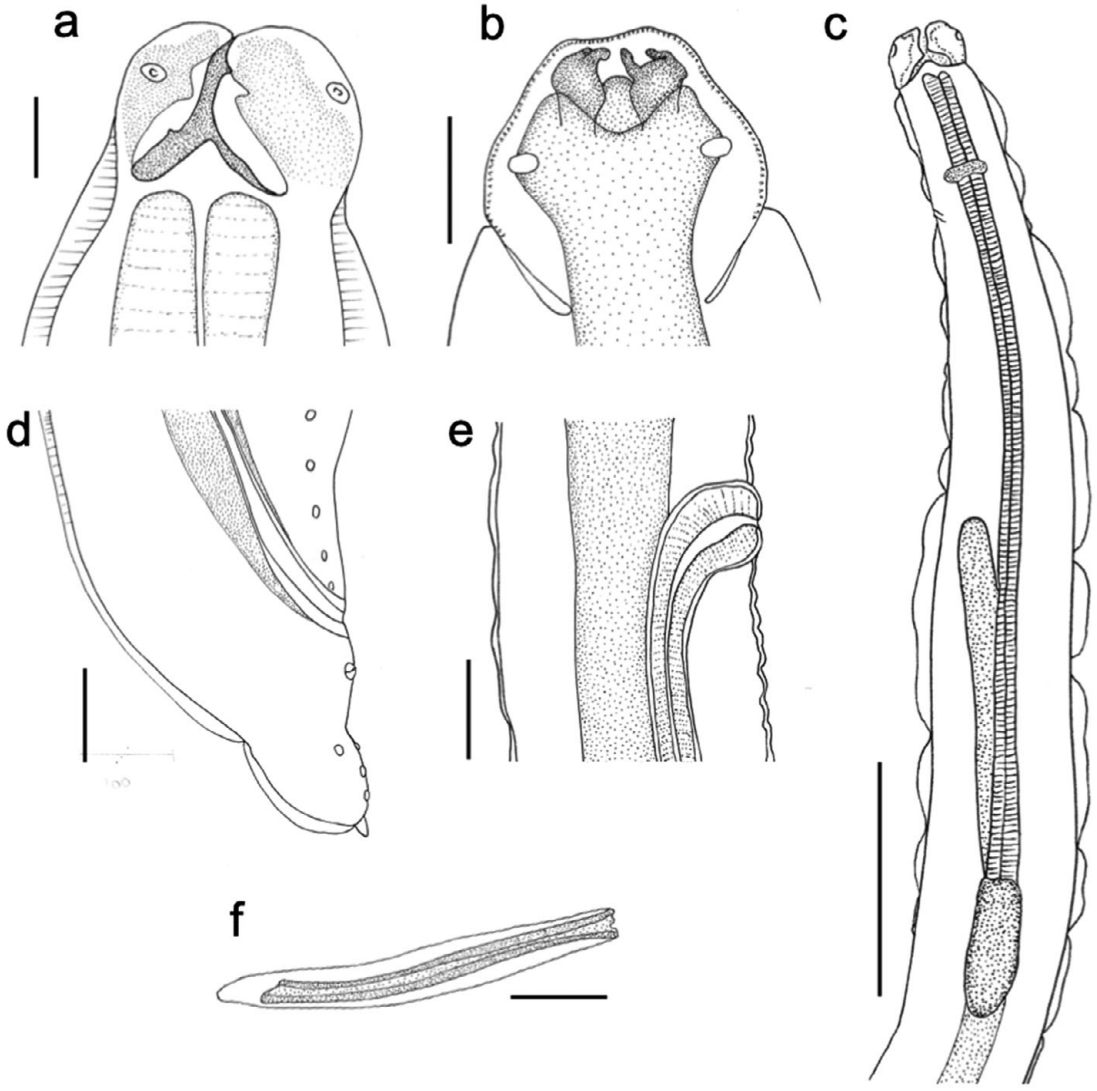

Figure 1. *Porrocaecum circinum* Johnston & Mawson, 1941. (a) Subventral lips and interlabia. (b) Dorsal lip showing labial pulp pattern. (c) Anterior extremity of female. (d) Posterior extremity of female. (e) Vulva of female, (f) Alate spicule of male. Scale bars: (a), (d) and (e) 100 μm; (b) 50 μm; (c) 1mm; (f) 200μm.

450–1300. Lips 179–265 long. Interlabia 84–101 long. Oesophagus 2.9–4.7 mm long, representing 5.7–11.0 % of BL. Nerve-ring and excretory pore 578–790 and 796–1012 respectively, from anterior extremity. Ventriculus 559–717 long. Intestinal caecum 1.55–2.94 mm long, representing 53–65 % of oesophageal length. Vulva pre-equatorial, at 33–40 % of BL. Vagina muscular, directed posteriorly from vulva (Figure 1e). Eggs oval, 98–110 × 74–88 (n = 12). Tail 353–528 long, without constriction. Phasmids not observed.

Localities. Waitati, Palmerston, Dunback, Waikouaiti, Dunedin, Waldronville, Harwood, Long Beach, Waihola, Berwick, Maungatua (all in Otago), Tekapo, Geraldine, Hinds, Temuka, St. Andrews, Timaru, Darfield (all in Canterbury).

Voucher specimens. Hologenophore Waihola, W.003970 Museum of New Zealand, Te Papa Tongarewa, Wellington, NZ

DNA sequences. har37nem1: ITS, OR827722; 18S, OR820168

Remarks

There are ten *Porrocaecum* species in the literature that have been found in raptors and which possess alae. *Porrocaecum accipiteri* Kumar & Gupta, 1977, *P. cheniella* Xu, 1957, *P. circum* Wang, 1965, *P. flammei* Karokhin, 1946, *P. pseudodepressum* Karokhin, 1946 and *P. skrjabini* Sultanov, 1946 have not been reported since being described, and are considered *species inquirendae* due to inadequate original descriptions. *Porrocaecum angusticolle* (Molin, 1890) Baylis & Daubney, 1922, *P. circinum* Johnston & Mawson, 1941, *P. depressum* (Zeder, 1800) Baylis, 1920, and *P. parvum* Li, Guo & Zhang, 2015 remain as the most closely comparable species to our specimens. The number of post-cloacal papillae (7 pairs) distinguishes *P. parvum* from our specimens (4 pairs) (Figure 2d). The metrics of *P. angusticolle* and *P. depressum* overlap in the most part with our specimens. However, the lip pulp of *P. angusticolle* is different in having two single projections and no bifurcations (Figure 2c), and the caecum comprises 66–84 % of oesophagus length in *P. angusticolle* but 53–66 % in the present specimens. *Porrocaecum depressum* is distinguished from the present specimens only by the number of post-cloacal papillae (5 pairs), but in all other respects the metrics overlap. However, despite similarity to both *P. angusticolle* and *P. depressum*, the molecular data clearly show that our specimens do not belong to those species. Although

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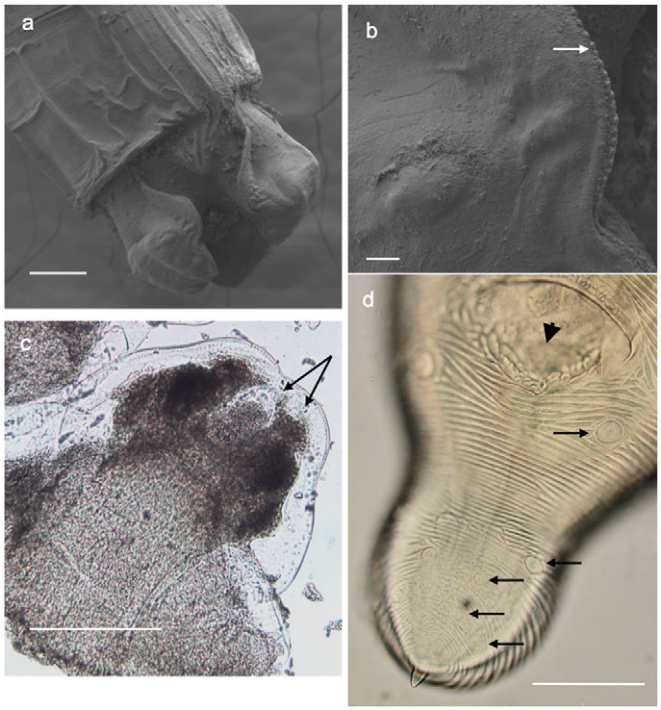

Figure 2. *Porrocaecum circinum* Johnston & Mawson, 1941. (a) Scanning electron micrograph of subventral lips and interlabia. (b) Close-up of subventral lip showing papilla and denticle border (arrow). (c) Light micrograph of a squash preparation of dorsal lip, showing labial pulp with digitiform processes (arrows). (d) Light micrograph of male posterior extremity showing post-cloacal papillae (small arrows) and rugose opening of cloaca (arrowhead). Scale bars: a), c) and d) 100 μm, b) 10μm.

detail was wanting in the original description of *P. circinum* and the specimens were apparently poor, our female specimens match well with the description (Johnston & Mawson 1941), and this, along with the geographical locality and the host species, leads us to place our specimens in *P. circinum.*

Genetic results

We obtained three ITS1 sequences of *P. circinum*, which were 100% identical at 496bp length. Our phylogenetic tree places a representative sequence within genus *Porrocaecum* with high nodal support (Figure 5a). Within *Porrocaecum,* species exhibit average 13.19% interspecific genetic divergence, with a range of 2.49–19.25%. *Porrocaecum circinum* was genetically closest to *Porrocaecum* sp. LC666446 ex *Haliaeetus albicilla* White-tailed eagle from Japan (3.11%) and *Porrocaecum angusticolle* MW447303 ex *Buteo buteo* common buzzard from Czech Republic (3.11%). We also obtained 18S sequences for six specimens of *P. circinum,* which were all identical. A BLASTn search and alignment (tree not shown) also placed our specimens within *Porrocaecum* and a close sister to *P. angusticolle,* with the other species forming an unresolved polytomy. Genetic distances were lower in the 18S gene (range 1–3% among *Porrocaecum* spp.).

Rhabditida Chitwood, 1933
Habronematoidea Ivaschkin, 1961
Habronematidae Ivaschkin, 1961
***Procyrnea* Chabaud, 1958**
***Procyrnea fraseri* n. sp. (Figure 3–4; Figure 6b)**
Synonym: *Procyrnea mansioni sensu* Mawson, 1968

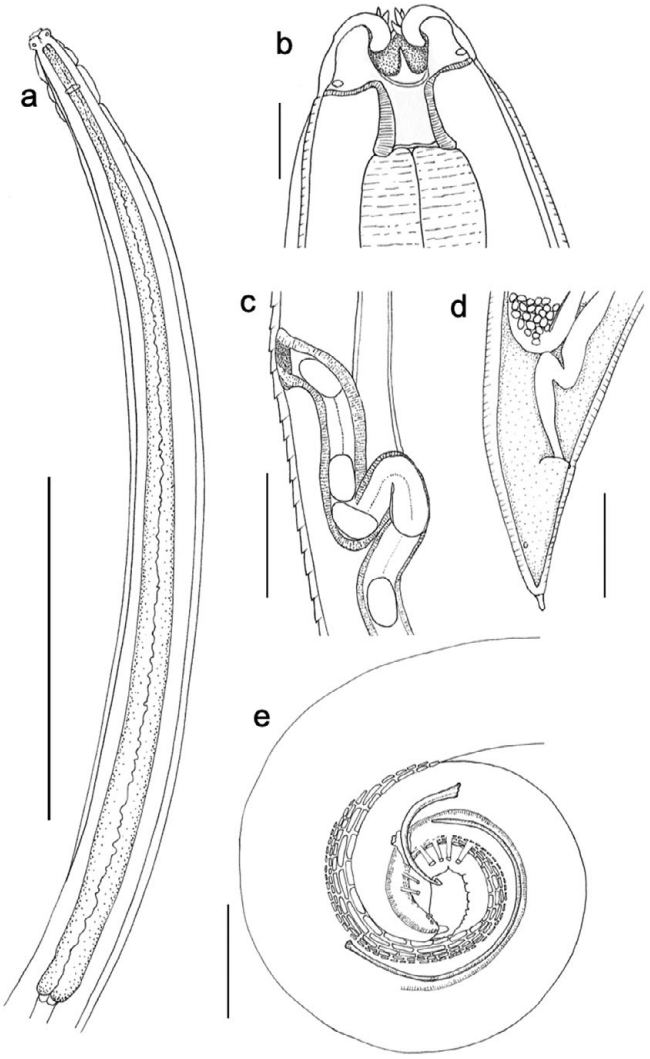

Figure 3. *Procyrnea fraseri* n. sp. (a) Anterior part of female. (b) Anterior extremity ventral view, (c) Region of vulva. (d) Posterior extremity of female. (e) Posterior extremity of male, showing coiled tail, spicules, gubernaculum and papillae. Scale bars: a) 1mm, b) 20μm, c) and d) 100μm, e) 200μm.

Specimens of a species of *Procyrnea* were found in 18% of birds examined, identifiable by paired pseudolabia with teeth inserted on the anterior border, lobes of sub-median labia simple in form, deirids in front of nerve ring and vulva in middle region of body, and "spirurid type" male tail characterised by 9 precloacal papillae, 4 postcloacal papillae and a terminal group of 8 papillae and 2 phasmids (Chabaud 2009). The worms were found in the proventriculus, and infections consisted of mature adults, all of a very similar size. Sexual size dimorphism was evident. Based on a literature search the specimens were adjudged to represent a new species of *Procyrnea*, and we therefore provide a description below.

General. Body small, exceptionally slender and straight, with fine transverse striations; females slightly larger than males. Paired lateral alae present, but not obvious on all specimens, asymmetrical in both length and width. Labial region consisting of two lateral pseudolabia and dorsal and ventral labia. Two lateral pseudolabia, narrow at base and greatly expanded distally, inner edge with three teeth; circular amphids located at base of pseudolabia. Dorsal and ventral labia each consisting of two submedian lobes, with two

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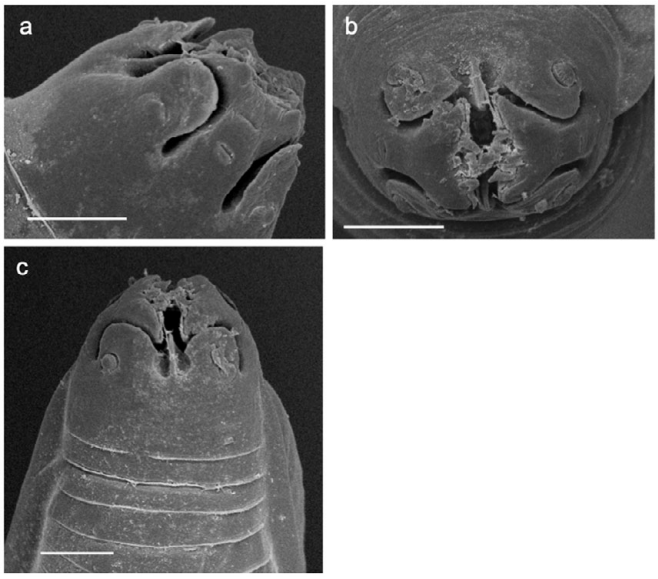

Figure 4. *Procyrnea fraseri* n. sp. (a) Scanning electron micrograph of anterior end, lateral view, showing pseudolabia with amphid. (b) En-face view showing medial teeth. (c) Ventral view showing bilobed labia with internal rib-like process, and papillae. Scale bars: a), b) and c) 10μm.

papillae on outer edges of each, and a median rib-like internal process. Lateral lobes of dorsal and ventral labia fit snugly into edges of lateral pseudolabia (Figure 3a, b, c). Buccal capsule sclerotized, walls thicker at base. Oesophagus divided into short anterior muscular part and long posterior glandular part: total oesophagus 17–27 % of BL, muscular part 10.9–18.9 % of total oesophagus. Nerve ring located at middle of muscular oesophagus; deirids anterior to nerve ring. Excretory pore posterior to nerve ring.

Male [Measurements based on 8 cleared specimens] Total body length 8–9.4 (8.9) mm; maximum width at mid-body region 144–175 (159.6) mm. Body length to width ratio, 1:50–60. Right hand lateral ala terminates level with end of oesophagus, left terminates approximately at two thirds BL. Buccal cavity 18–23 (19.3) long. Muscular oesophagus 274–375 (345.4) long, maximum diameter at anterior region 20–30 (25.7); glandular oesophagus 1.5–2.0 (1.9) mm long, maximum diameter at posterior region 72–93 (81.3). Oesophagus 21–27 (25) % total BL. Deirids at 126–174 (154), nerve-ring at 183–244 (216) from anterior extremity. Posterior extremity strongly ventrally curled, with torsion creating asymmetry; tail rounded with small mucron, 14–16 long. Bilateral caudal alae present, with prominent longitudinal interrupted ridges on ventral surface. Cloacal aperture 129–151 (140) from posterior extremity. Four pairs of pedunculate pre-cloacal papillae arranged symmetrically; two pairs of pedunculate post-cloacal papillae arranged asymmetrically (Figure 3e). Four pairs of sessile papillae and one pair of phasmids located near the tail tip. Single pre-cloacal papilla not observed. Spicules unequal and dissimilar; left spicule fine, 532–590 (560) long with thin, tapering tip; right spicule short, thick 233–258 (243) long, curved, with barb at distal end. Ratio BL: left and right spicule length, 1:0.06 and 1:0.03, respectively. Ratio left spicule: right spicule length 1:2.2–2.4 (1:2.3). Gubernaculum present, shape irregular, 45–50 long.

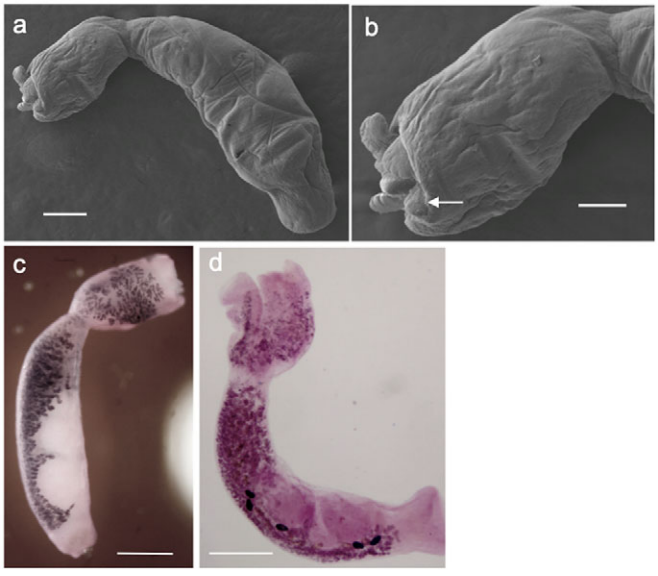

Figure 5. *Strigea falconis* Szidat, 1928. (a) Scanning electron micrograph of whole worm. (b) Prosoma showing oral sucker exposed at anterior edge of holdfast (arrow). (c) Light micrograph of lightly stained whole worm, top lit. (d) Light micrograph of stained specimen. Scale bars: a) 200μm, b) 100μm, c) and d) 500μm

Female [Measurements based on 7 cleared specimens, and one SEM specimen] Total body length 10.9–15.7 (13.8) mm; maximum width at mid-body region 140–282 (236.9) mm. Body length to width ratio, 1:51–78. Right hand lateral ala terminates level with end of oesophagus, left terminates slightly posterior to level of vulva (Figure 3a). Buccal cavity 22–25 (23) long. Muscular oesophagus 411–467 (424.6) long, maximum diameter at anterior region 30–35 (32.5); glandular oesophagus 2.2–2.5 (2.4) mm long, maximum diameter at posterior region 99–107 (102). Oesophagus 17–22 (19) % total BL. Deirids at 123–196 (166.3), nerve-ring at 251–258 (254.5), excretory pore at 360 (n=1) from anterior extremity. Ovaries didelphic, uteri opisthodelphic. Uterine vagina muscular; vulva without prominent lips, opening a transverse slit in mid-body region, at 5.4–7.2 (6.4) mm (42–45% BL) from anterior extremity (Figure 3c). Anus opening a transverse slit; tail 180–280 (215) long (Figure 3d). Paired phasmids near caudal end; tail sharply pointed or with small mucron. Eggs small, oval 32–39 x 18–22, with thick, smooth shell, embryonated.

Type host. Australasian harrier *Circus approximans* (Peale)

Type locality. Burkes Pass, Canterbury, South Island, New Zealand. 44°05′25″S 170°36′00″E

Other localities. Roxburgh, Waikouaiti (both in Otago), Tekapo, Omarama, Hinds, Studholme, Timaru port (all in Canterbury)

Site of infection. Stomach

Prevalence and intensity. In 12 of 65 birds (18%), mean intensity 5.42 worms per bird, range 1 to 30.

Type material. Holotype male W.003966, Allotype female W.003967, Paratypes 3 specimens W.003968 deposited with the Museum of New Zealand, Te Papa Tongarewa, Wellington, NZ.

Voucher material. Hologenophore, from har15nem1, Roxburgh W.003969.

Representative DNA sequences. har15nem1: 18S, OR820169

Zoobank reference. urn:lsid:zoobank.org:act:ACA74521-3CEA-459F-B543-1F95F36DFFF4

Etymology. The species is named for Jenni Fraser who runs the rescue and rehabilitation centre at the NZ Raptor Trust, and shared with us the bodies of those birds that didn't make it. The Trust is a non-profit organisation that, as well as caring for sick and injured birds, aims to educate and inspire current and future generations, raising awareness and boosting populations of New Zealand's vulnerable birds of prey.

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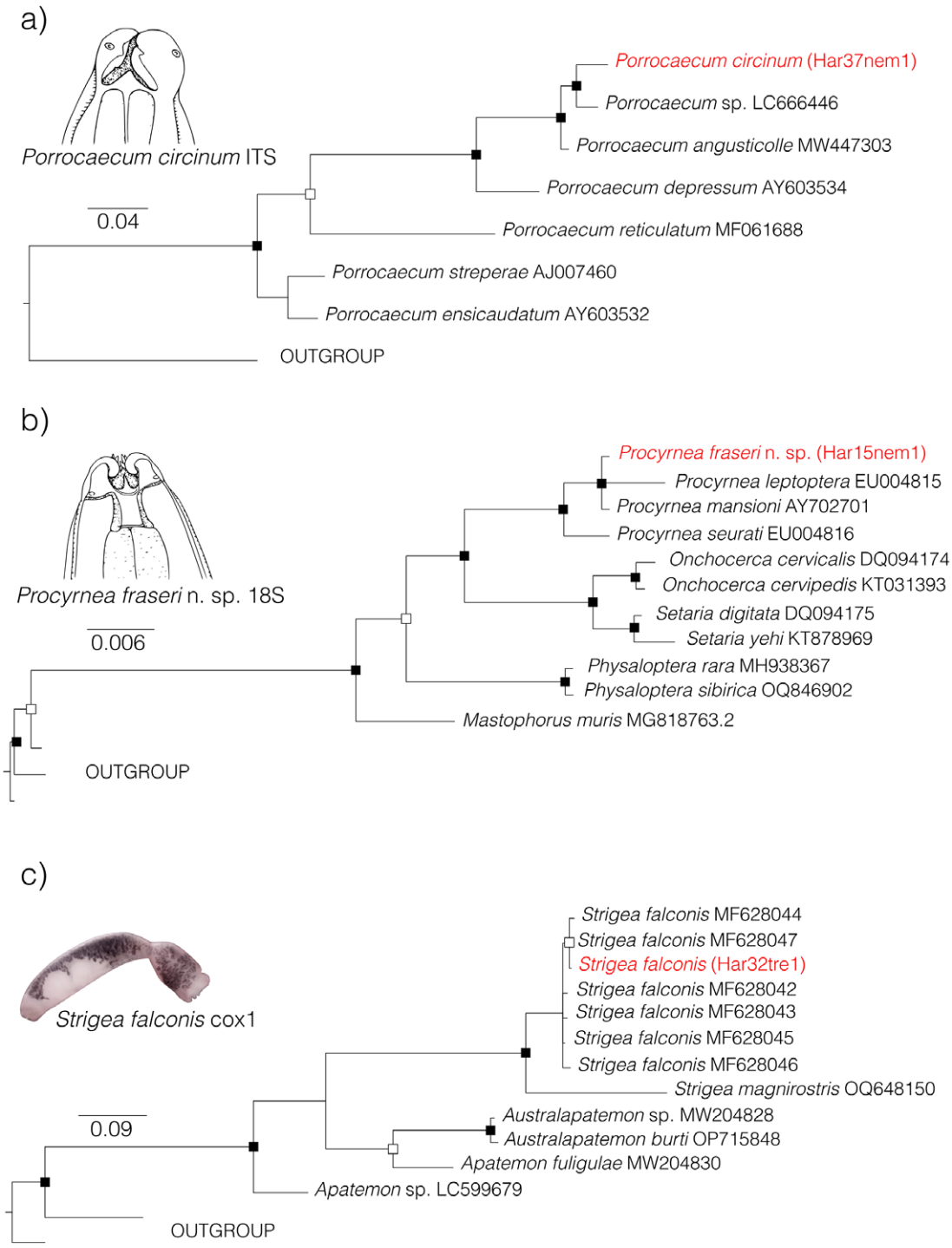

Figure 6. 50% majority rule consensus trees resulting from Bayesian phylogenetic inference of a) ITS gene for species belonging to *Porrocaecum* (outgroup includes *Toxocara cati* KY003067), b) 18S gene for species belonging to *Procyrnea* (outgroups include *Porrocaecum angusticolle* EU004820 and *Porrocaecum reticulatum* MF072700), and c) *cox*1 gene for species belonging to Strigeidae (outgroups include *Diplostomum alascense* MZ323250 and *D. ardeae* NC049068). Red sequences represent newly produced sequences in this study. Bayesian Posterior Probability (BPP) illustrated by black (strongly supported, 0.95-1.0) and black-outlined (moderately supported, 0.8-0.95) squares.

Remarks

In possessing two, asymmetrical lateral alae, the specimens described above are comparable to *Procyrnea americana* (Chandler, 1941), *P. buckleyi* (Bisseru, 1955), *P. dolichocolpos* (Chabaud & Brygoo, 1958), *P. incerta* (Smith, Fox & White, 1908), *P. magnipapillata* (Ali, 1961) and *P. mansioni* (Seurat, 1914).

However, these specimens are very slender, with a width in length ratio of 1: 50–78, whereas all comparable species are all similar in length but much stouter, with a width in length ratio of 1: 27–43 throughout the six species. In addition, the spicules of the new species are much shorter than in all of these species (spicule length is not given for *P. incerta*). The vulva position of *P. incerta* is

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closer to the anterior than in *P. fraseri* n. sp. (33% of BL as opposed to 41–52% BL).

In addition to these factors *P. buckleyi* has spicules that are uniquely shaped with the left shorter than the right, and the species is found in bustards (Otitidae). *Procyrnea magnipapillata* has particularly robust caudal papillae, a prominent vulva and six pairs of papillae on the tail tip of the male which differentiates it from *P. fraseri* n. sp. *Procyrnea dolichocolpos* has an enormously long left spicule, over 6mm, and *P. americana* possesses only a single pair of post-cloacal pedunculate papillae.

The new species is closest in morphology to *P. mansioni.* However, the difference in length: width ratio (1:35–43 as opposed to 1:50–78 in *P. fraseri* n. sp.), along with the proportion of the oesophageal length (0.25–0.33% of BL as opposed to 0.21–0.27% in *P. fraseri*, n. sp.) and spicule lengths (L680 and, R315 as opposed to L532–590 and R233–258 in *P. fraseri* n. sp.) distinguish *P. fraseri* from *P. mansioni.*

The original description of *P. mansioni* (Seurat 1914) discussed specimens from Brazil, but the species has apparently been recovered from accipitriform hosts also in India (Ali 1961), Africa (Quentin *et al.* 1983; Gendre 1922) and Australia (Mawson 1968). However, the identity of some reports may be questionable: spicule sizes of *P. mansioni* given by Ali (1961) and Quentin *et al.* (1983) are sufficiently different from Seurat's (1914) description to query the identification of their specimens. In Australia, Mawson (1968) reported *P. mansioni* from hosts brown falcon *Falco berigora* Vigors & Horsfield, whistling kite *Haliastur sphenurus* (Vielliot) and grey goshawk *Accipiter novaehollandiae* (Gmelin). Mawson's measurements, too, disagree with those of Seurat's original description. Her description of the Australian specimens do, however, compare very closely with the metrics from our New Zealand specimens and this, along with the known recent origin of the New Zealand harrier in Australia, suggests that the specimens described in Mawson's paper were probably the same as ours, and we provisionally place *P. mansioni sensu* Mawson (1968) in synonymy with *P. fraseri* n. sp.

Genetic results

Our newly generated 18S sequence of *Procyrnea fraseri* n. sp. was grouped with other species of *Procyrnea,* with high nodal support (Figure 5b). Genetic distances among the species of *Procyrnea* ranged from 0.00–1.34% (mean distance of 0.67%). *Procyrnea fraseri* n. sp. was identical to a specimen identified as *P. mansioni* (AY702701) except for the addition of three insertions in the *P. mansioni* sequence. We suspect these differences may be ambiguous sites as no other habronematid representatives had those three insertions. Unfortunately the *P. mansioni* sequence was not associated with a publication, so it is not possible to confirm the identification, origin or host from which it was taken. It appears that variability is very low in the 18S gene. An attempt to sequence ITS1 was unsuccessful.

TREMATODA Rudolphi, 1808

Diplostomida Olson, Cribb, Tkach, Bray, and Littlewood, 2003

Diplostomoidea Poirier, 1886

Strigeidae Railliet, 1919

***Strigea* Abildgaard, 1790**

***Strigea falconis* Szidat, 1928 (Figure 5a–d; 6c)**

Synonyms:

Amphistoma falconis palumbi (Viborg, 1795) Rudolphi, 1809*; A. striatum* Rudolphi, 1809*; A. macrocephalum* Rudolphi, 1819*; Festucaria strigis* Frölich, 1802*; Holostoma variabile* Nitzsch, 1819*; Holostomum variabile* Nitzsch, 1819*; H. cornu* Hausmann, 1899*; Neostrigea africana* Bisseru, 1956; *Strigea elongata* Furmaga, 1957, and Oshmarin, 1963, *nec* Yamaguti, 1935*; S. falconis* var. *brasiliana* Szidat, 1929*; S. falconis* var. *meleagris* Harwood, 1931*; S. falconis falconis* Szidat, 1928*; S. f. palumbi* Viborg, 1795*; S. ornithocystis* Lutz, 1929.

A total of 35 specimens of strigeid trematode attributable to genus *Strigea* were found in 6 (9%) of 65 harriers examined. They were identifiable by their bipartite body, vitellaria distributed in both prosoma and opisthoma (terminology follows Achatz *et al.* 2022), large oral and ventral suckers, well-developed pharynx, holdfast organ reaching to anterior margin of prosoma, testes multilobed in posterior part of opisthoma, oval ovary and large copulatory bursa, with genital cone delimited and surrounded by muscular ring (Niewiadomska 2002). The worms were found in the intestine, and infections included only mature adults. A combination of morphometric features and genetic identity confirmed these specimens to be *S. falconis.* Characteristic features are shown in Figure 5a–d and a brief description follows.

Measurements from 8 stained and mounted specimens. Total length 2.6–3.8 (3.3) mm; body distinctly bipartite; maximum width at level of ventral sucker. Tegument smooth (Figure 5a). Prosoma cup-shaped, usually asymmetrical; 782–1161 (953) long, 515–653 (592) wide. Opisthoma subcylindrical, lightly curved dorsally, flared at genital cone; usually widest at level of anterior testis; 1731–2650 (2289) long, 470–665 (565) wide. Prosoma to opisthoma length ratio 1:1.93–2.99 (1:2.41). Oral sucker terminal; 109–143 (127) long, 109–134 (121) wide. Prepharynx absent. Pharynx 97–112 (107) long, 103–134 (108) wide. Ventral sucker in midprosoma; 145–262 (215) long, 163–203 (190) wide. Oral to ventral sucker width ratio 1: 1.43–1.83 (1.59). Proteolytic gland lobed, overall a longitudinal oval, at base of prosoma slightly anterior to constriction; 173–206 (185) long, 109–152 (138) wide. Ovary bilobed; 169–268 (214) long, 156–205 (177) wide. Ovary positioned 30–43 (34) % length of opisthoma. Laurer's canal long, broad and convoluted. Mehlis' gland intertesticular. Testes tandem, with large lobes. Anterior testis 314–450 (384) long, 280–455 (347) wide; anterior margin positioned 39–45 (42)% length of opisthoma. Posterior testis 263–484 (401) long, 266–477 (373) wide; anterior margin positioned 55–65 (59) % length of opisthoma. Seminal vesicle highly convoluted, post-testicular. Vitellarium in both parts of body; in prosoma invading all lobes of holdfast organ, absent in intersegmental constriction, in opisthoma ventral to testes, ending anterior to genital cone. Uterus ventral, with few large eggs; eggs 89–99 (92) long, 55–65 (61) wide.

Localities. Long Beach, Waikouaiti (both in Otago), Burkes Pass, Studholme (both in Canterbury).

Voucher specimens. Hologenophore, from Long Beach W.003971

DNA sequences. har32tre1: *cox*1 OR826952; 28S OR827721; NAD OR842556. har9tre1: 28S OR827720

Remarks

The new specimens were compared against all congeners by consulting the original descriptions. When considering the overall size, posterior extent of the vitellaria, length of the 'neck', size of the suckers, size of the genital cone, size of the pharynx, bird host taxa and geographical origin, the specimens from the Australasian

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harrier were closest to *Strigea falconis* as originally described by Szidat (1928). This conclusion was supported by the finding of 100% genetic identity (*cox1* and *nadh1*) with *S. falconis* from various hosts in Czech Republic (Heneberg *et al.* 2018).

Genetic results

Our phylogeny illustrates high nodal support for our newly generated *cox*1 sequence being grouped within *Strigea falconis* (Figure 5c). The genetic divergence of *cox*1 sequences within *S. falconis* ranged from 0.00–1.69% (mean distance 1.03%) and our newly generated sequence was 100% identical to *S. falconis* sequence MF628047 ex *Circus aeruginosus* Western marsh harrier in Czech Republic in 2013 (Heneberg *et al.* 2018). The interspecific genetic divergence between *Strigea falconis* and *S. magnirostris* was 10.9%. No phylogenetic tree was produced for *nadh*1 gene, but our newly produced sequence matched 100% to the same individual that compared 100% at *cox*1 (Heneberg *et al.* 2018).

CESTODA Rudolphi, 1808
Cyclophyllidea van Beneden in Braun, 1900
Paruterinidae Fuhrmann, 1907
Cladotaenia Cohn, 1901
***Cladotaenia anomalis* Presswell & Bennett, 2023**

A number of long, fragile cestodes were found in the intestines of 37 (57%) harriers examined, at intensities of 1 to >15. These were placed in the genus *Cladotaenia* and were formally described and named as *C. anomalis* due to the unusual arrangement of hooks in the rostellum. Specimens lack the second row of hooks that is characteristic of this genus, but in all other respects conformed to the diagnosis of *Cladotaenia*, which was supported by molecular evidence. These cestodes were found in birds from all over the southern South Island, and it was conjectured that the intermediate hosts were most likely to be house mice, and may have originated from southern Asia (Presswell & Bennett 2023a).

ACANTHOCEPHALA Koehlreuther, 1771
Polymorphida Petrochenko, 1956
Polymorphidae Meyer, 1931
***Polymorphus* Lühe, 1911**
***Polymorphus circi* Presswell & Bennett, 2023**

A total of 50 acanthocephalans was found in the intestines of 4 (6%) harriers examined, at intensities of 1 to 40. These were placed in the genus *Polymorphus* and were formally described and named as *P. circi* after the genus name of the host, it being an unusual host for the genus, which generally includes aquatic amphipods as part of the life cycle. Specimens were distinguished from all other species by their proboscis hook arrangement (20–22 rows of 11–13 hooks), as well as absence of sexual dimorphism, trunk size, proboscis shape and egg size. These acanthocephalans were found in birds from areas with the potential to support freshwater, brackish or marine amphipods, but as yet the actual intermediate hosts are unknown (Presswell & Bennett 2023b).

Discussion

We found six helminth species infecting our sample of Australasian harriers from South Island, New Zealand: 3 nematodes (*Porrocaecum circinum*, *Procyrnea fraseri* n. sp. and a fragmented capillariid), one trematode (*Strigea falconis*), one cestode (*Cladotaenia anomalis*) and one acanthocephalan (*Polymorphus circi*). Prior to this study there was only one helminth parasite recorded from the harrier in New Zealand (a species of Capillariidae) and no records from the remainder of its Australasian range. Below we discuss what is known of the life cycles of the parasites, their potential origins and pathogenicity.

Porrocaecum circinum

The presence or absence of alae and their symmetry or asymmetry are an important diagnostic character for *Porrocaecum* species. Accordingly, the type specimens of *Porrocaecum circinum* were examined for us by Leslie Smales of South Australia Museum who was able to confirm that they possessed alae, although this was not in the original description (Johnston & Mawson 1941). The original description stated that the denticles surrounding each lip continued nearly to the base of the lip, identical to the condition in the New Zealand harrier specimens, but differing from other closely related species. This may be an established species of *Porrocaecum* in raptors in Australia, as Johnston and Mawson (1941) reported it also from the little eagle *Hieraaetus morphnoides* (Gould) and the white goshawk *Accipiter novaehollandiae* (Gmelin). Placement of our specimens in this species may be confirmed or refuted if more specimens from Australia become available for morphological and molecular comparison.

The life cycle of *Porrocaecum* spp. includes an earthworm as intermediate host, and some species are known to use small mammals as paratenic hosts (Fagerholm & Overstreet 2008) where they encyst in the mesenteries and body cavity. It is not known whether *P. circinum* in New Zealand utilises paratenic hosts, or whether harriers include earthworms in their diet. Earthworms have not been mentioned as prey in any of the harrier diet studies for New Zealand (Baker-Gabb 1981, Carroll 1968, Douglas 1970, Redhead 1968), so it seems likely that larval stages utilise small mammals as paratenic hosts.

Procyrnea fraseri

Only a single species of *Procyrnea* has previously been reported from New Zealand; *P. kea* Clark, 1978 was recovered from a New Zealand kea *Nestor notabilis* Gould. *Procyrnea kea* is distinguished by having symmetrical alae, bifurcated barbs on the tip of the long spicule, a left spicule over 6 times as long as that of *P. fraseri* n. sp. and a right spicule approximately twice the length of that of *P. fraseri* n. sp. No complete natural life cycle is known for any *Procyrnea* species. However, larvae have been found or experimentally developed in beetles (Velikanov 1988), and orthopterans (Quentin *et al.* 1983). In terms of paratenic hosts, one study found larvae of *P. mansioni* encapsulated in the stomach wall of toads *Bufo bufo asiaticus* (Hsu and Chow 1938), and a range of reptiles as well as a hedgehog were infected with *P. zorillae* (Velikanov 1988).

These small nematodes were found embedded in the mucosa of the proventriculus, but never in very large numbers, and although it is unlikely that this species could cause deleterious pathology in the harrier, there is at least one case in the literature where a species of *Procyrnea* in large numbers has proved lethal (Siegel *et al.* 2012).

Strigea falconis

Strigea falconis has appeared in the literature on countless occasions, in reports mainly from Western Eurasia, but also from USA

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and Brazil. Dubois (1968), who scrutinised all reports in the literature, listed 41 citations for the species, which he identified as subspecies *S. falconis falconis*. The identity of the species in many accounts may be questionable, as *S. falconis* is an unremarkable species of the genus with no outstanding features. *Strigea* species are almost always found in raptors and it is possible that specimens found in past studies were placed in *S. falconis* by default. Interestingly, the New Zealand specimens, although genetically identical in *cox1* and *nadh1* to Heneberg *et al.*'s (2018) specimens from Czech Republic, were smaller in the means of all metrics, although the mean ratios of prosoma to opisthoma and ventral sucker width to oral sucker width were near identical. Dubois recorded *S. falconis* from *Falco berigora* Vigors & Horsfeld (as *Hieracidea orientalis* Sharpe), in Australia (Dubois 1937), but later redesignated the specimens as *S. glandulosa* Dubois, 1937 (Dubois & Pearson 1965), thus leaving no record of *S. falconis* originating from Australia.

Strigea species have an unusual obligatory four-host life cycle. As well as the usual first intermediate host (a snail), the life cycle includes a nonencysted stage between the cercaria and metacercaria, the mesocercaria. This infects the second intermediate host, a larval amphibian. There is a third intermediate host (an amphibian, reptile, bird or mammal), in which the developing larva encysts as a metacercaria, and this is ingested by a bird of prey with the host wherein it matures to adult. All four hosts are needed to complete the life cycle (Blasco-Costa & Locke 2017). Although the intermediate hosts of *S. falconis* in New Zealand are not known, one, at least, must be an introduced frog. New Zealand has only three species of native frog and these have extremely restricted distribution and are not found widely in South Island where our samples originated from. The most likely hosts are therefore southern bell frog *Ranoidea raniformis* (Keferstein), introduced from Tasmania in 1867 (Vörös *et al.* 2008), or the brown tree frog *Litoria ewingi* (Dumeril and Bibron), introduced from Tasmania in 1875 and now widespread in South Island (NZHS 2021). Particularly notable is the fact that this latter frog species is highly cold-tolerant and tadpoles can be found throughout the year (Cree 1984), thus extending the potential cycle for any parasite requiring it as a host. The question arises, is the distribution of *S. falconis* constrained by the second, or third, intermediate host in New Zealand? As the third intermediate host could be a frog, a lizard, a mammal or water bird, all of which are known to prey on tadpoles, the answer is not clear, and surveys of the introduced fauna are required. However the life cycle is maintained, the species presumably could not have arrived prior to the introduction of frogs from Australia in the late 1800s.

Cladotaenia anomalis

An unnamed specimen of *Cladotaenia* from *Ci. approximans* in Victoria was listed as present in the Australian Helminth Collection (now South Australia Museum) (Mawson *et al.* 1986), and specimens of *C. circi* from *Ci. approximans* in Vanuatu are in the Natural History Museum, London. Apart from these specimens, there are no previous records of any cestode from the Australasian harrier (Presswell & Bennett 2023a).

Polymorphus circi

In Australasian harriers, only one acanthocephalan has been reported in Australia (*Centrorhynchus asturinus* (Johnston, 1913)) (Smales 2003), and until now, no records existed for the New Zealand populations. Acanthocephalan parasites comprise a relatively small phylum of dioecious helminths that can have significant impacts on their host's health (e.g. Shanebeck *et al.* 2022). In New Zealand, acanthocephalan burdens in seabird hosts from the Family Polymorphidae have recently been associated with isolated cases of mortality due to peritonitis (Presswell and Bennett 2021).

Capillariidae gen. sp.

In addition to those helminths listed herein, fragments of a capillariid nematode were found in one bird. No attempt at identification was possible as the pieces were in poor condition, the infection site was not clear and DNA amplification was unsuccessful, so the identity of this worm remains unknown. Alley *et al.* (2004) reported a capillariid species in the mouth of a harrier, which was associated with mycobacterial infection typical of avian tuberculosis. They suggested that this was a common finding. Mirza (2014) also found capillariids in 13.3% of harriers, and French *et al.* (2020) reported finding capillariids in 13 harriers (prevalence not known), which were placed in genus *Eucoleus* genetically. All of our birds were examined under the tongue, and in the oral cavity and oesophagus, but no capillariids, lesions or ulcers were found. It should be noted that all previous records are from the North Island, or north of the South Island. It is possible the presence of capillariid infections is confined mainly to the northern region, and it is rare or absent in the south.

Other remarks

Five of the six helminths found in the gastrointestinal tract of the harriers examined potentially utilise small mammals in their life cycle. All mammals in New Zealand (except for two rare species of endemic bat) have been introduced to the country within the last two hundred years. The exception to this is the Polynesian rat, which arrived with Polynesian colonists approximately 800 years ago, and which is now restricted to the south of South Island (https://www.doc.govt.nz/nature/pests-and-threats/animal-pests/rats). Based on their ubiquitous distribution and prey potential, the most obvious contenders for intermediate or paratenic hosts are small mammals: brown rat *Rattus norvegicus*, black rat *Rattus rattus*, mouse *Mus musculus* and hedgehog *Erinaceus europaeus*. Nineteen helminth parasites are reported from these hosts (McKenna 2010, 2018), but none of the worms found in the harrier is among them.

Frogs may be paratenic hosts for *Procyrnea fraseri* n. sp., and second (or even third) intermediate hosts for *Strigea falconis*. As the only possible anuran hosts in the South Island are the two species introduced from Australia, this constrains the arrival of these helminths to the latter part of the nineteenth century. In summary, it appears that the harriers that first colonised New Zealand arrived without parasites, but acquired them from introduced vertebrates after European colonisation. It seems a thorough review of the parasites of introduced small vertebrates in New Zealand is required.

Data availability statement. Not applicable.

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Ethics. Receipt and handling of deceased birds in this study complies with a Department of Conservation permit 65658–DOA awarded to the authors.

Code availability. Not applicable.

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