DOI: 10.2478/s11686-011-0015-0

Acta Parasitologica, 2011, 56(2), 213–226; ISSN 1230-2821

VERSITA

Camallanus Railliet et Henry, 1915 (Nematoda, Camallanidae) from Australian freshwater turtles with descriptions of two new species and molecular differentiation of known taxa

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Abstract

Two new species of *Camallanus* are described from Australian freshwater turtles. *Camallanus beveridgei* sp. nov. is reported from *Elseya dentata* in Northern Territory. It differs from other species of the genus parasitic in turtles by several characters including the shape of the median ridge in the buccal capsule and the position of the anterior pair of caudal papillae in males. *Camallanus sprenti* sp. nov. is reported from *Elseya latisternum* (type host) and *Emydura krefftii* in northern Queensland. It is closely related to *Camallanus tuckeri*, and differs from the latter species in possessing a shorter oesophagus. We summarize data on morphology, distribution and specificity of 5 known *Camallanus* spp. from Australian turtles and provide a key for their identification. Sequence comparison of more than 500 base pairs at the 5' end of the nuclear 28S rDNA gene confirms the status of *C. sprenti* and *C. beveridgei* as new species. *Camallanus sprenti* differs from the other 4 species of *Camallanus* from Australian turtles by 16–59 bases (3.1–11.5%) while *C. beveridgei* differed from the other 4 species by 23–60 bases (4.5–11.6%). Phylogenetic analysis demonstrates close interrelationships among *C. tuckeri*, *C. sprenti* and *C. beveridgei*, the three species with most similar buccal capsules.

Keywords

Nematoda, *Camallanus*, Australia, turtles, rDNA, molecular differentiation

Introduction

Camallanidae Railliet et Henry, 1915 is a globally distributed nematode family consisting primarily of parasites of fishes. Some species are known from amphibians and reptiles, including turtles (Ivashkin *et al*. 1971, Petter 1979). Yeh (1960) erected the genus *Serpinema* Yeh, 1960 which includes turtle parasites with characteristic buccal capsules that possess a gap between the dorsal and ventral groups of ridges on each of the buccal capsule valves. Baker (1983) described *Camallanus chelonius* Baker, 1983 from the South-African side-necked turtle *Pelusios sinuatus* (Pleurodira, Pelomedusidae). This parasite lacked such a buccal capsule gap and was, therefore, allocated into *Camallanus* Railliet et Henry, 1915. *Camallanus chelonius* was later reported from the Australian side-necked turtles *El. latisternum* and *Emydura macquarii* in Queensland (Ferguson and Smales 1998). However, Rigby *et al*. (2008) determined that this report was the result of misidentification and described two *Camallanus* species, *C. nithoggi* Rigby et Sharma, 2008 and *C. waelhreow* Rigby et Sharma, 2008, parasitizing *El. latisternum*, *Emydura krefftii* and *Em. macquarii* in Queensland. Recently, Kuzmin *et al*. (2009) described *C. tuckeri* Kuzmin, Tkach et Snyder, 2009 from *Emydura australis* and *Chelodina burrungandjii* in Western Australia.

As part of a survey of the parasite fauna of Australian freshwater turtles we have identified two previously undescribed *Camallanus* species, one from *El. dentata* in Northern Australia, and another from *El. latisternum* and *Em. krefftii* in Queensland. In addition, we have found *C. waelhreow* and *C. nithoggi* from previously unreported hosts and localities. The present work includes descriptions of the new species as well as a survey of known records of all 5 species of *Camallanus* from Australian freshwater turtles and a key to their identification. Molecular differentiation of all *Camallanus* species from Australian turtles and phylogenetic analysis of

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their interrelationships based on partial sequences of nuclear large ribosomal subunit (28S) gene are also provided.

Materials and methods

In May and June, 2005, freshwater turtles were collected by hand in the Daly River, Northern Territory (NT), Australia and examined for helminths. In July, 2007, 5 turtle species taken in baited traps in northern Queensland (QLD) were similarly examined (see Table II for collection locales and coordinates). Collections proceeded under permits issued from the Parks and Wildlife Commission of the Northern Territory and the Queensland Environmental Protection Agency. Turtles were euthanized using sodium pentabarbitone and turtle bodies were deposited at the Queensland Museum and the Museum and Art Gallery of the Northern Territory. Numerous camallanids were obtained. For comparative morphological study we used specimens of *C. tuckeri* (type series, 3 males and 14 females, Queensland Museum Nos. G231372–G231377), *C. waelhreow* collected from *Em. macquarii* and *Chelodina expansa* in Queensland and New South Wales (NSW) (15 males and 10 females), and *C. nithoggi* collected from *El. latisternum* in Queensland (6 males and 7 females).

Upon recovery from the host intestine the nematodes were rinsed in saline, killed with hot 70% ethanol and stored in 70% ethanol. For light microscopy they were cleared in phenol-glycerine (1:3 ratio). Measurements were taken from a compound microscope using digital imaging and Rincon measurement software (v. 7.1.2, Imaging Planet, Goleta, California). All measurements are in micrometers unless otherwise stated.

Genomic DNA for molecular analysis was extracted according to Tkach and Pawlowski (1999) from tissue taken from the middle of the body of each nematode specimen while the taxonomically important anterior and posterior regions were preserved as vouchers for morphological identification. DNA was extracted from 1 specimen of *C. beveridgei* sp. nov. obtained from *El. dentata* from the type locality (Daly River, NT), and 3 specimens of *C. sprenti* sp. nov., each from a different specimen of *El. latisternum* collected from Cobbold Gorge, Einasleigh River and Hann River Roadhouse, Queensland (Table II). For molecular comparison and phylogenetic analysis, we used previously published DNA sequences (Kuzmin *et al*. 2009) of *C. tuckeri* (GenBank Nos. FJ969492–FJ969497), *C. nithoggi* (FJ969498), and *C. waelhreow* (FJ969499–FJ969505). For outgroup comparison, we sequenced a specimen of *Serpinema octorugatum* (Baylis, 1933) collected from *Cuora amboinensis* in Thailand.

Fragments of DNA spanning the 3' end of 18S nuclear rDNA gene, internal transcribed spacer region (ITS1 + 5.8S + ITS2) and 5' end of the 28S gene were amplified by PCR on an Eppendorf Master Gradient thermal cycler according to Kuzmin *et al*. (2009). Forward primer c1740f (5'-TGAAA ATCCTCCGTGCTCGG-3') and reverse primer n900r (5'-GGTTCGATTAGTCTTTCGCC-3') were used for PCR. PCR primers and additional internal primers 300R (5'-CAACTT TCCCTCACGGTACTTG-3') and ECD2 (5'-CTTGGTC-CGTGTTTCAAGACGGG-3') were used for sequencing. PCR products were purified directly using Qiagen Qiaquick™ (Valencia, CA) columns, cycle-sequenced using ABI BigDye™ chemistry, alcohol-precipitated, and run on an ABI Prism 3100™ automated capillary sequencer. The ITS region of *C. beveridgei* sp. nov. could not be sequenced despite numerous attempts and different approaches used. Therefore, sequences of about 500 bp long fragment at the 5' end of the 28S gene were used in our analyses. The seqeunces were assembled using Sequencher™ (GeneCodes Corp., ver. 4.1.4) and submitted to GenBank: *C. beveridgei* sp. nov. (HQ730893), *C. sprenti* sp. nov. (HQ730894-HQ730896) and *Serpinema octorugatum* (HQ730897).

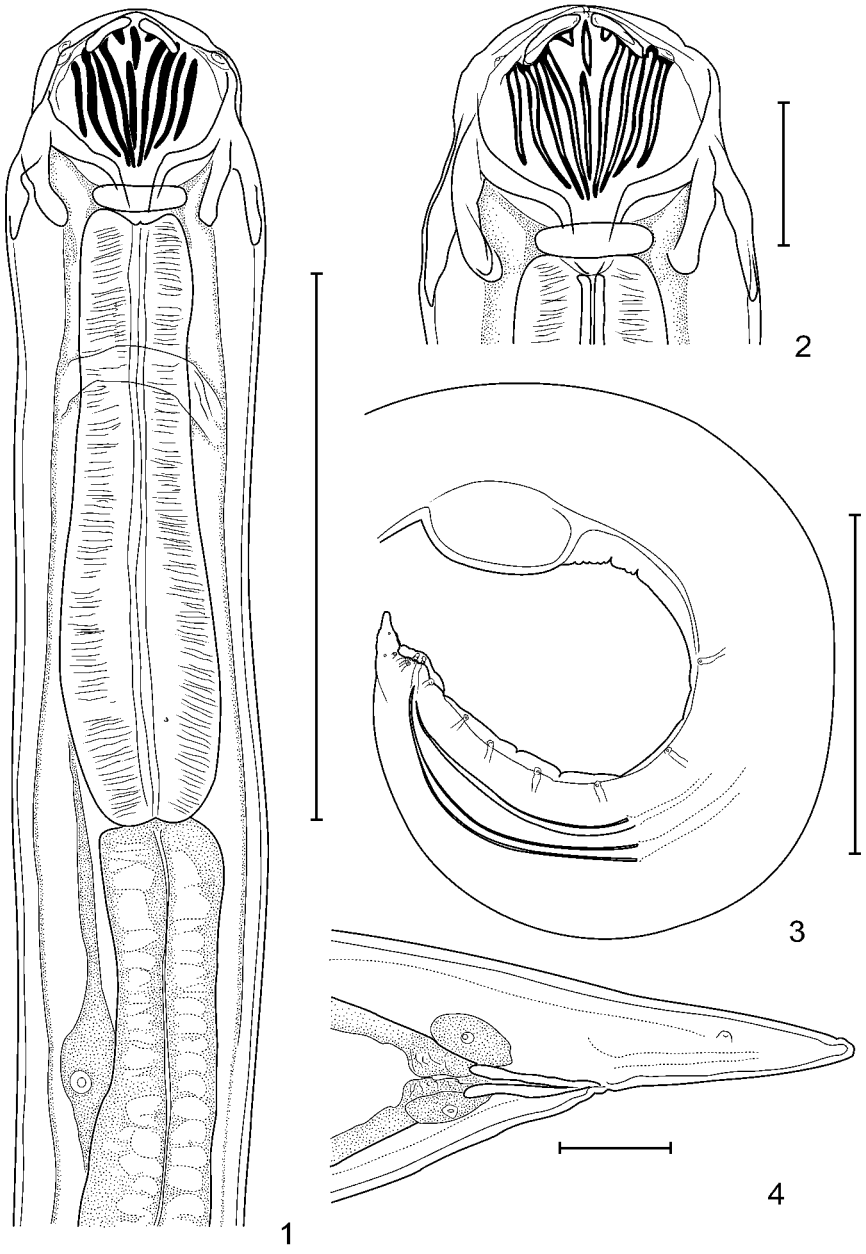
Sequences were aligned for pairwise comparison in the BioEdit program, version 7.0.1 (Hall 1999). Since multiple sequences within each species were identical, only one representative sequence was used for the pairwise comparison and phylogenetic analysis for each species. No sites were excluded from the analysis as ambiguously aligned. Maximum likelihood analysis of these data was performed using the exhaustive search, random sequence addition, and TBR branch-swapping options of PAUP* (v. 4.0b10) (Swofford D.L. 2001; PAUP*: Phylogenetic Analysis Using Parsimony [and other methods]), Version 4.0b10. Sinauer, Sunderland, Massachusetts. Gaps were treated as fifth base. Nodal support was assessed using bootstrap resampling (1,000 bootstrap replicates, 100 heuristic searches per replicate.

Results

***Camallanus beveridgei* sp. nov.**

Description (Figs 1–4, 9, 11, 12, 27–32)

General: Three males and 7 females of the new species were studied and selected as type series. Slender worms. Body cuticle finely transversely striated. Head end rounded, tail end tapering. Oral opening narrow, slit-like, with rounded corners. Eight circumoral papillae present: 4 minute papillae in the inner circle and 4 large, rounded, in the outer circle. Outer papillae situated very close posteriorly to corresponding inner papillae. Buccal capsule consisting of 2 valves and a basal ring. Each buccal capsule valve with 11–14 ridges; some ridges may be more or less shortened. A median ridge consisting of shorter, tooth-like anterior part and longer posterior part almost reaching posterior edge of valve; the two parts separated by short gap (Fig. 2); occasionally posterior part split into 2 shorter ridges (Fig. 32). Two submedian ridges, nearest to a median one, short, often tooth-like. From



Figs 1–4. *Camallanus beveridgei* sp. nov.: **1** – anterior part of the body, lateral view; **2** – head end, lateral view; **3** – tail end of male, lateral view; **4** – tail end of female, lateral view. Scale bars = 0.5 mm (1 and 3), 0.1 mm (2 and 4)

4 to 5 complete ridges present in dorsal and ventral groups; a short, incomplete 6th ridge observed in one specimen (Fig. 30). Differences in number of ridges in males and females were not detected. Thick sclerotized ring present at base of buccal capsule. Tridents prominent, with posterior ends slightly behind level of buccal capsule basal ring. Muscular oesophagus cylindrical. Glandular oesophagus about 1.6–2.3 times longer than muscular one. Deirids minute, papilla-shaped, situated somewhat anterior to level of posterior end of muscular oesophagus. Excretory pore not observed. Intestine straight, narrow. Rectum thin-walled. Tail without mucrons in both sexes.

Males (measurements of the holotype [2 paratypes]): Body 15.09 (14.63, 15.10) mm long, 223 (189, 231) wide. Posterior part of body coiled ventrally. Buccal capsule valves 147 (137, 149) long (measured from anterior edge to basal ring) and 148 (160, 162) wide in lateral view. Total length of buccal capsule 172 (187, 188). Sclerotized ring at base of buccal capsule 76 (83, 86) wide and 24 (26, 27) long. Middle prong of tridents 112 long (measured in 1 male). Nerve ring at 290 (285, 288) from anterior end. Deirids at 608 from anterior end of body and at 107 from posterior end of muscular oesophagus (measured in one male). Muscular oesophagus 536 (516, 543) long, glandular oesophagus 886 (918, 941) long. Distance from an-

terior end of body to posterior end of oesophagus 1.59 (1.64, 1.65) mm or 10.6 (10.9, 11.2)% of body length.

Spicules almost equal in length and shape, left spicule slightly shorter and less sclerotized (Figs 3, 12). Right spicule 493 (421, 425) long. Posterior part needle-shaped, slightly curved ventrally. Left spicule, 458 (354, 365) long. Spicule length ratio 1.08 (1.15, 1.20). Anterior ends of invaginated spicules at about midlength of preanal part of genital alae.

Genital alae ventrolateral, low, elevated in anterior part and joined on ventral side. Posterior edges of alae posterior to midlength of tail. In preanal part, alae supported by 7 pairs of pedunculate papillae (Figs 3, 11). Anterior pair of preanal papillae situated far posterior to anterior elevation of alae. Two pairs of ventrolateral pedunculate postanal papillae supporting alae. Two pairs of subventral papillae situated close to first postanal ventrolateral pair. Four minute subventral sessile papillae (a pair of preanal and a pair of postanal) present. Phasmids lateral, papilla-shaped, situated at midlength of tail. A pair of minute ventral papillae situated close to tail end. Tail conical, with rounded end. Tail length 103 (75, 105) or 0.7 (0.5, 0.7)% of body length.

Females (measurements of 7 paratypes, limits): Body 25.82−32.03 mm long, 282−424 wide. Buccal capsule 191–220 long, valves 157−170 long and 170−195 wide. Sclerotized ring at base of buccal capsule 94−108 wide, 19–25 long. Middle prong of tridents 125 long (measured in 1 female). Muscular oesophagus 599−690 long, glandular oesophagus 1.03−1.43 mm long. Distance from anterior end of body to posterior end of oesophagus 1.88–2.26 mm or 6.8–8.2% of body length. Nerve ring at 306–348 from anterior end.

Vulva pre-equatorial, 9.86−11.63 mm from anterior end (36.3–39.6% of body length), with prominently elevated anterior lip (Fig. 9). Tail short, conical, 162−278 long (0.6–1.0% of body length), with rounded tip (Fig. 4). Phasmids situated at midlength of tail.

Taxonomic summary

Type host: *Elseya dentata* (Gray). Prevalence 67%, intensity 3.75 (3−6).

Type locality: Daly River (13°44´S, 130°41´E), Northern Territory, Australia.

Site of infection: Intestine.

Type series: 3 males (holotype and 2 male paratypes) and 7 female paratypes.

Type specimens deposited: Holotype (male): Queensland Museum, Brisbane, Australia QM G231378. Paratypes: QM G 231379–231382; Harold W. Manter Laboratory, Lincoln, Nebraska, USA, HWML 64567–64568.

Etymology: The species is named in honor of Prof. Ian Beveridge (University of Melbourne) in recognition of his contributions to helminthology in general, and his contribution to our knowledge of the Australian nematode and cestode faunas in particular.

Remarks

Camallanus beveridgei sp. nov. is closely related to other 4 *Camallanus* species from Australian turtles. The new species is morphologically most similar to *C. nithoggi*, sharing the presence of a large anterior lip of the vulva (an elevation of the body wall anterior to the vulva) in females. *Camallanus beveridgei* sp. nov. differs from all 4 species (*C. waelhreow*, *C. nithoggi*, *C. tuckeri* and *C. sprenti* sp. nov.) in the shape of median ridge of the buccal capsule. Only in *C. beveridgei* sp. nov. is the ridge divided into a short, tooth-like anterior part and longer posterior part. The anterior pair of the caudal papillae in *C. beveridgei* sp. nov. is situated posterior to the anterior elevation of the genital alae, whereas in the other 4 species these papillae are situated at the level of the elevation. *Camallanus beveridgei* sp. nov. is the largest species among known *Camallanus* spp. from Australian turtles (Table I). However, it possesses the shortest tail relative to other species, both in males (0.5–0.7% to body length) and females (0.6–1.0% to body length) (Table I).

Pairwise sequence comparison of about 500 bp fragments at the 5’ end of the 28S nuclear ribosomal DNA gene of *Camallanus beveridgei* sp. nov. and 4 other known species of *Camallanus* from Australian turtles strongly supported the status of *C. beveridgei* sp. nov. as a new species. The levels of sequence difference were substantial, from 23 bases (4.5%) between *C. beveridgei* sp. nov. and *C. sprenti* sp. nov. to 60 bases (11.6%) between *C. beveridgei* sp. nov. and *C. waelhreow* (Table III). No intraspecific variability was detected in the sequenced fragment in 4 *Camallanus* species for which we obtained more than one sequence.

***Camallanus sprenti* sp. nov.**

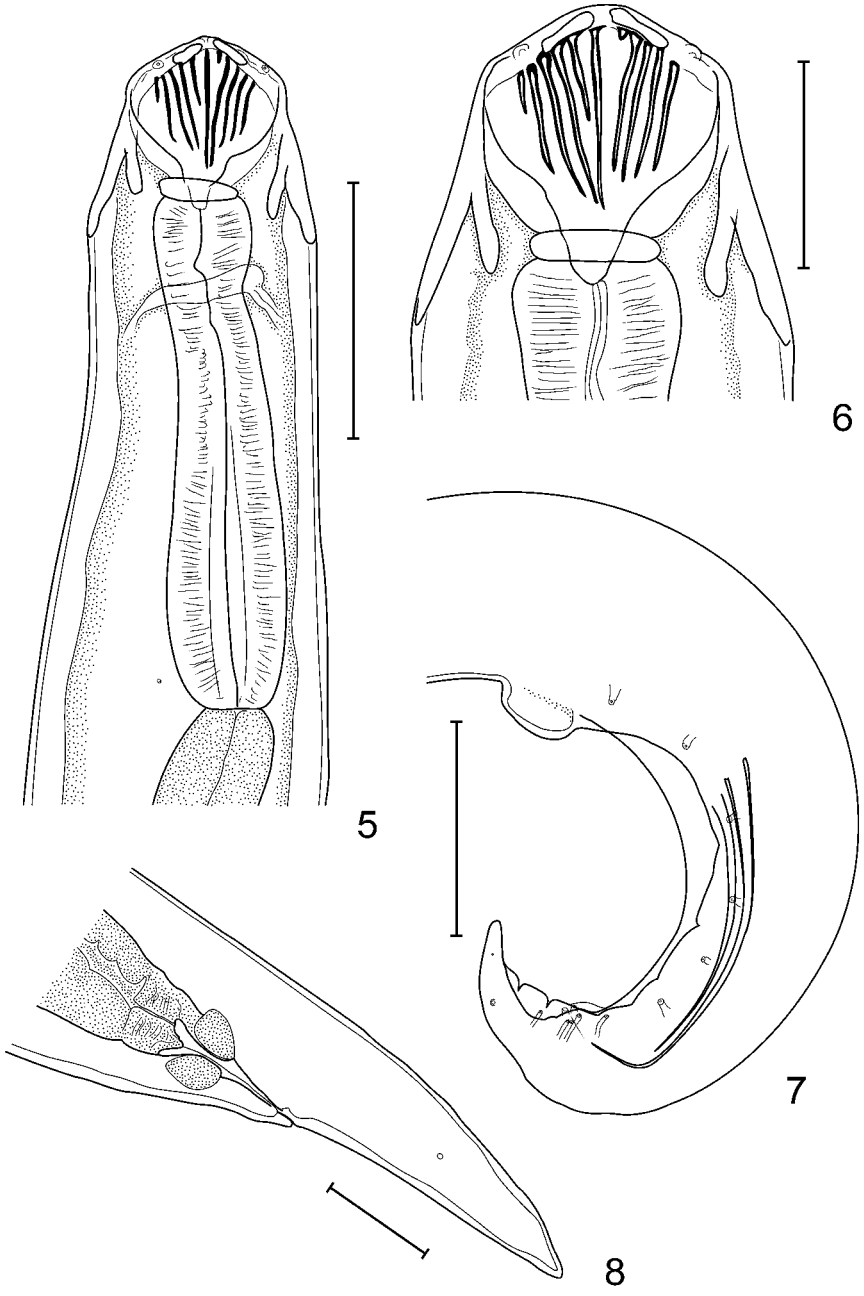
Description (Figs 5–8, 10, 13, 14, 33, 34): Eight males and 7 females of the new species were studied; 9 fully gravid specimens (4 males and 5 females) were measured.

General: Slender worms. Anterior end rounded, posterior end tapering. Body cuticle finely striated transversely. Oral opening slit-like, with rounded corners. Eight cephalic papillae surrounding oral opening arranged in 2 circles: 4 minute papillae of inner circle and 4 large rounded papillae of outer circle. Outer papillae situated very close posteriorly to corresponding inner papillae. Buccal capsule valves usually with 9–11 ridges: a central ridge plus 2 groups (dorsal and ventral) of 4–5 ridges. In dorsal and ventral groups, 1 or 2 ridges may be incomplete, shortened posteriorly (Fig. 34). Dorsal and ventral ridges angled medially from anterior to posterior (Fig. 6). One or two short, incomplete ridges may be present beside central ridge. No difference in number of ridges in males and females.

Dark-coloured sclerotized ring present at base of buccal capsule. Buccal capsule supported by ventral and dorsal tridents. Trident prongs approximately equal in length; ends of prongs posterior to level of sclerotized ring.

Table I. Morphometry of 5 *Camallanus* spp. from Australian freshwater turtles. Means are followed by limits in parentheses

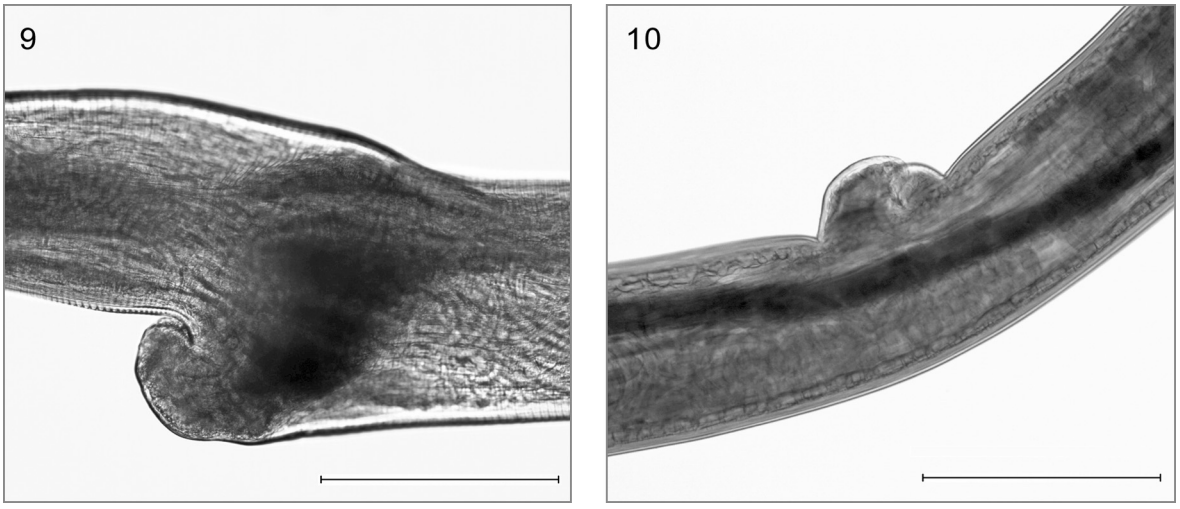
Characters	***C. waelhreow*** (16 males and 10 females)	***C. nithoggi*** (6 males and 7 females)	***C. tuckeri*** (3 males and 11 females)	***C. beveridgei*** (3 males and 7 females)	***C. sprenti*** (4 males and 5 females)
Body length, mm					
males	8.50 (6.90–10.05)	10.56 (8.01–12.56)	11.25 (10.20–11.89)	14.94 (14.63–15.09)	11.66 (10.85–12.43)
females	14.09 (12.91–16.02)	17.87 (16.69–19.12)	16.37 (12.92–19.03)	28.01 (25.81–32.03)	23.59 (22.66–24.25)
Body width					
males	160 (115–191)	208 (165–249)	183 (164–195)	214 (189–231)	234 (202–263)
females	229 (182–278)	277 (195–322)	232 (159–275)	347 (282–424)	394 (360–422)
Valves of buccal capsule (BC) length					
males	110 (101–115)	100 (93–105)	121 (113–129)	144 (137–149)	115 (104–120)
females	117 (114–125)	113 (108–118)	143 (135–153)	163 (157–170)	137 (133–141)
BC width					
males	98 (92–102)	118 (114–121)	119 (115–125)	157 (148–162)	117 (111–121)
females	113 (107–121)	135 (125–143)	149 (137–179)	186 (170–195)	147 (145–148)
BC length:width ratio					
males	1.1 (1.1–1.2)	0.8 (0.8–0.9)	1.0 (1.0–1.1)	0.9 (0.8–1.0)	1.0 (0.9–1.0)
females	1.0 (0.9–1.1)	0.8 (0.8–0.9)	1.0 (0.8–1.1)	0.9 (0.8–0.9)	0.9 (0.9–1.0)
Width of sclerotized ring at base of BC					
males	64 (59–72)	65 (60–71)	74 (67–78)	82 (76–86)	74 (72–77)
females	74 (66–80)	72 (68–76)	88 (75–94)	101 (94–108)	90 (87–94)
Glandular to muscular oesophagus (OE) length ratio					
males	1.5 (1.3–1.7)	1.7 (1.6–1.8)	1.7 (1.6–1.8)	1.7 (1.7–1.8)	1.9 (1.8–2.0)
females	1.6 (1.5–1.6)	2.0 (1.8–2.1)	1.6 (1.2–1.9)	1.9 (1.6–2.3)	2.0 (2.0–2.1)
Distance from anterior body end to posterior end of Oe as % of body length					
males	15.3 (12.9–18.7)	11.6 (10.6–14.1)	13.9 (13.1–15.0)	10.9 (10.6–11.2)	10.9 (10.4–11.4)
females	10.7 (9.8–11.5)	7.9 (7.3–8.7)	10.8 (9.8–11.9)	7.2 (6.8–8.2)	7.2 (6.7–7.5)
Tail length					
males	121 (112–138)	122 (102–140)	186 (177–194)	94 (75–105)	183 (177–188)
females	232 (201–249)	252 (230–276)	254 (201–249)	229 (162–278)	295 (277–318)
Tail length as % of body length ratio					
males	1.4 (1.2–1.6)	1.2 (1.0–1.3)	1.7 (1.5–1.9)	0.6 (0.5–0.7)	1.6 (1.4–1.6)
females	1.7 (1.4–1.9)	1.4 (1.2–1.7)	1.6 (1.4–1.8)	0.8 (0.6–1.0)	1.2 (1.1–1.3)
Right spicule length	514 (484–542)	489 (451–522)	388 (381–394)	446 (421–493)	369 (345–392)
Right spicule length to left spicule length ratio	1.3 (1.2–1.4)	1.6 (1.4–1.8)	1.2 (1.2–1.2)	1.1 (1.1–1.2)	1.4 (holotype)



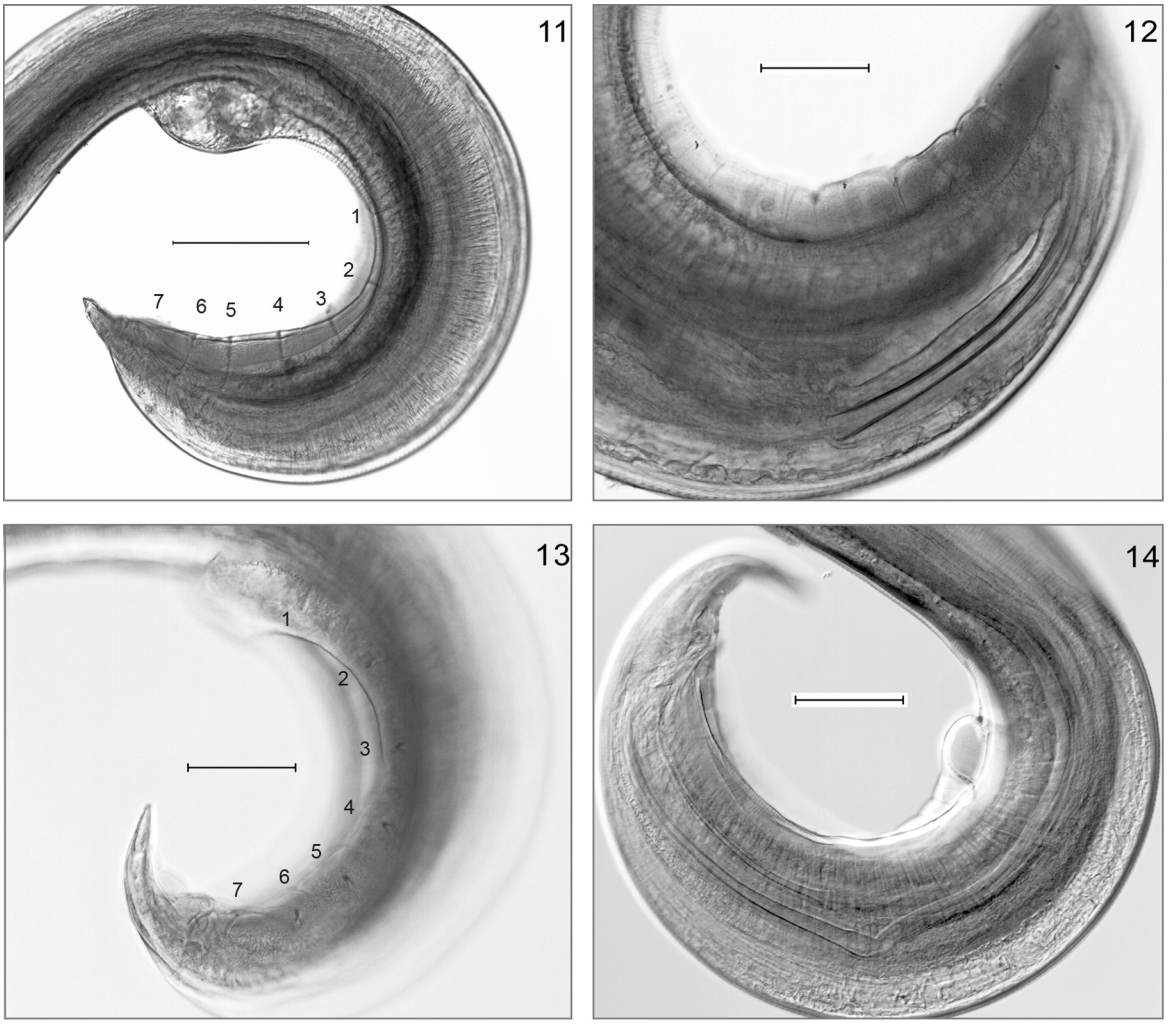
Figs 5–8. *Camallanus sprenti* sp. nov.: **5** – anterior part of the body, lateral view; **6** – head end, lateral view; **7** – tail end of male, lateral view; **8** – tail end of female, lateral view. Scale bars = 0.2 mm (5 and 7), 0.1 mm (6 and 8)

Muscular oesophagus wide, club-shaped. Glandular oesophagus 1.8–2.0 times longer than muscular one. Three prominent large nuclei at posterior end of glandular oesophagus. Nerve ring situated close to anterior end of oesophagus. Deirids minute, papilla-shaped, situated somewhat anterior to border between muscular and glandular oesophagus. Excretory pore not observed. Intestine straight, narrow. Rectum straight, thin-walled. Tail without mucrons in both sexes.

Males (measurements of the holotype and limits for 3 paratypes in parentheses). Body 10.89 (11.48–12.43) mm long and 202 (225–263) wide. Posterior end curved ventrally. Buccal capsule 125 (137–140) long, 115 (111–121) wide. Length of buccal capsule valves 104 (116–120). Sclerotized ring at base of buccal capsule 77 (72–74) wide and 21 (20–21) long. Middle prong of tridents 108 long (measured in one male). Muscular oesophagus 396 (377–414) long, glandular oesophagus 713 (689–806) long. Distance from anterior end of body to posterior end of glandular oesophagus 1.234 (1.203–1.359) mm or 11.4 (10.4–11.4)% of body length. Nerve ring at 186 (190–195) from anterior end. Deirids situated 104 anterior to posterior end of muscular oesophagus (measured in 1 male).

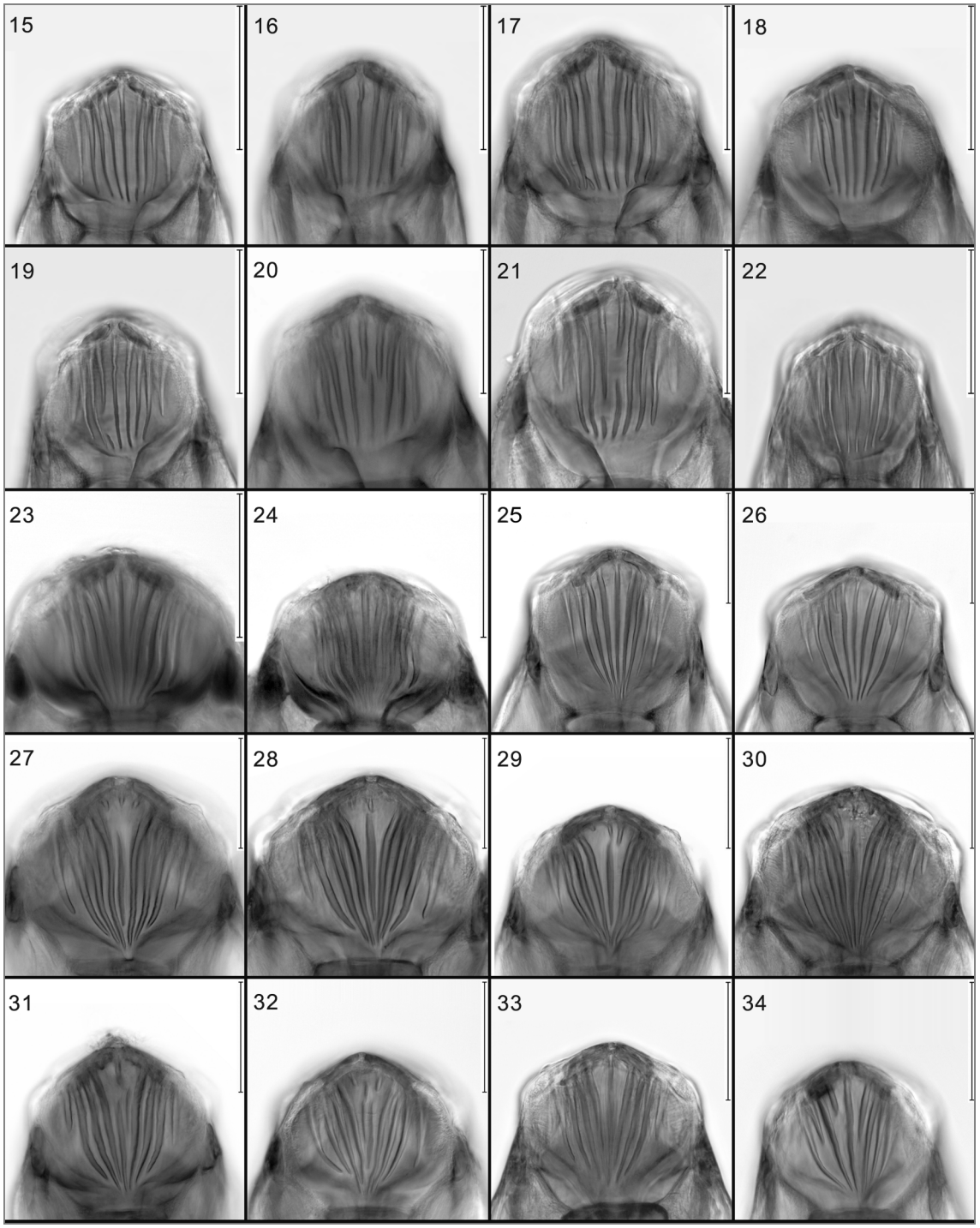


Figs 9 and **10.** Body near vulva in *Camallanus beveridgei* sp. nov. (**9**) and *Camallanus sprenti* sp. nov. (**10**); lateral view. Scale bars = 0.5 mm



Figs 11–14. Tail end in males of *Camallanus beveridgei* sp. nov. (**11**, **12**) and *Camallanus sprenti* sp. nov. (**13**, **14**). **11** and **13** – position of precloacal caudal papillae; **12** and **14** – shape and position of spicules. Precloacal ventrolateral papillae associated with genital alae are numbered from anterior to posterior. Scale bars = 0.5 mm (11), 0.1 mm (12–14)

Genital alae ventrolateral, low, elevated in anterior part and joined on ventral side. Posterior edges of alae posterior to midlength of tail. In preanal part, alae supported by 7 pairs of pedunculate papillae (Figs 7, 13). Anterior pair of preanal papillae situated at posterior part of elevation of genital alae. Two pairs of ventrolateral pedunculate postanal papillae supporting alae. Two pairs of subventral papillae situated close to first postanal ventrolateral pair. Four minute subventral sessile papillae (a pair of preanal and a pair of postanal) present. Phasmids lateral, papilla-shaped, situated at midlength of tail. A pair of minute ventral papillae situated close to tail end. Spicules unequal (Figs 7, 14). Right spicule larger and more sclerotized,



Figs 15–34. Variability of head end morphology in different *Camallanus* spp. from Australian freshwater turtles: **15–22** – *C. waelhreow*; **23**, **24** – *C. nithoggi*; **25**, **26** – *C. tuckeri*; **27**–**32** – *C. beveridgei* sp. nov.; **33**, **34** – *C. sprenti* sp. nov. Scale bars = 0.1 mm

392 (345–373) long; left spicule 276 long. Spicule length ratio 1.80 (1.80–2.03). Proximal parts of spicules needle-shaped.

Tail 177 (178–188) long, or 1.6 (1.4–1.6)% of body length.

Females (measurements of 5 paratypes, limits). Larger than males, body 22.66–24.25 mm long, 360–422 wide at mid-length. Buccal capsule 153–164 long, 145–148 wide; valves 133–141 long. Sclerotized ring 87–94 wide and 20–23 long. Middle prong of tridents 117 long (measured in one female). Muscular oesophagus 488–517 long, glandular oesophagus 977–1.092 long. Distance from anterior end of body to posterior end of oesophagus 1.630–1.757 mm, or 6.7–7.5% of body length. Nerve ring at 238–248 from anterior end. Deirids at 533 from anterior end of body, or at 132 anterior to posterior end of oesophagus (measured in one female).

Vulva pre-equatorial, at 8.11–9.57 mm from anterior end (33.4–40.2% of body length). Vulva lips elevated, rounded. Anterior lip much larger than posterior one (Fig. 10). Elevation of both lips present both in non-gravid and gravid specimens. Tail conical, elongated, 277–318 long (1.1–1.4% of body length). Tail tip rounded, with rough surface (Fig. 8).

Taxonomic summary

Type host: *Elseya latisternum* (Gray). Prevalence 73%; intensity 3.7 (1–9).

Other hosts: *Emydura krefftii* (Gray). Prevalence 11%; intensity 8.5 (1–16).

Type locality: Hann River Roadhouse (15°11´S, 143°52´E), Queensland.

Other localities: Wenlock Billabong (13°05´S, 142°56´E); Lake Tinaroo (17°15´S, 145°35´E); Cobbold Gorge (18°48.77´S, 143°23.44´E); Einasleigh River (18°30´S, 144°06´E), all in Queensland, Australia.

Site of infection: intestine.

Type series: 15 specimens, 8 males (holotype and 7 male paratypes) and 7 female paratypes.

Type specimens deposited: Holotype (male): Queensland Museum, Brisbane, Australia QM G232215. Paratypes: QM G232216–232221; Harold W. Manter Laboratory, Lincoln, Nebraska, USA, HWML 66667.

Etymology: The species is named in honor of Prof. John Sprent (University of Queensland) for his contributions to nematology and particularly to the knowledge of nematodes of Australian reptiles.

Remarks

Camallanus sprenti sp. nov. is similar to other 4 *Camallanus* species from Australian turtles in number of male caudal papillae, body size and proportions. The new species is most simi-

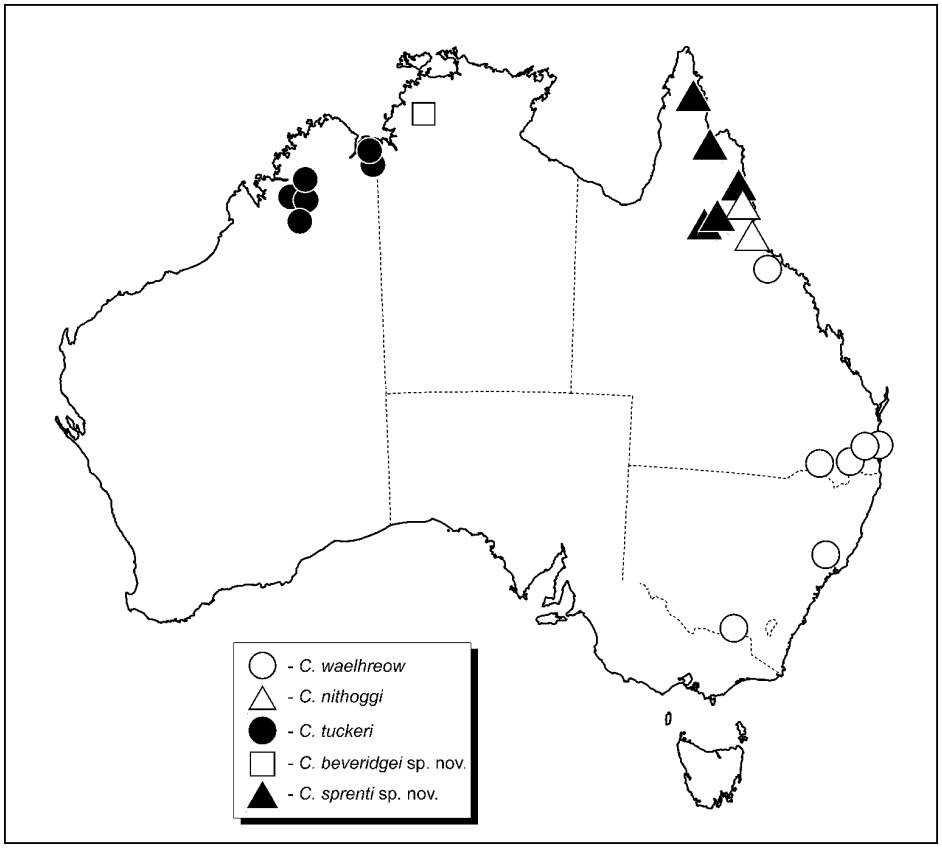


Fig. 35. Distribution of *Camallanus* spp. from freshwater turtles in Australia

Table II. Hosts and localities of 5 *Camallanus* spp. from Australian freshwater turtles

Parasite species	Host species	Localities	Source of information
C. waelhreow	*Em. macquarii*	Halpine Dam, Brisbane, QLD (27°14′S, 153°01′E)	present study
		UQ Farm Dam, Brisbane, OLD (27°31′S, 152°55′E)	present study
		Leslie Dam, Warwick, QLD (28°13′S, 151°55′E)	present study
		MacIntyre Br, Inglewood, QLD (28°27′S, 150°57′E)	present study
		Mungabareena Reserve, Albury, NSW (36°05′S, 146°56′E)	present study
		Leslie Dam, QLD (28°1′S, 152°55′E)	Rigby *et al*. (2008)
	Em. macquarii dharra	Smith Creek, QLD (31°53′S, 151°55′E)	Rigby *et al*. (2008)
	Em. krefftii	Jurona Station, QLD (19°33′S, 147°16′E)	Rigby *et al*. (2008)
	Ch. expansa	Mungabareena Reserve, Albury, NSW (36°05′S, 146°56′E)	present study
C. nithoggi	*El. latisternum*	Platypus Creek, QLD (17°21′S, 145°35′E)	present study
		Paluma Dam (18°57′S, 146°10′E)	Rigby *et al*. (2008)
C. tuckeri	*Em. australis*	Kununurra, WA (15°47′S, 128°42′E)	Kuzmin *et al*. (2009)
		Argyle Lake Spillway, WA (16°07′S, 128°44′E)	Kuzmin *et al*. (2009)
		Bell Creek, WA (17°10′S, 125°21′E)	Kuzmin *et al*. (2009)
		Geike Gorge, WA (18°06′S, 125°42′E)	Kuzmin *et al*. (2009)
	Ch. burrungandjii	Kununurra, WA (15°47′S, 128°42′E)	Kuzmin *et al*. (2009)
		Donkey Hole, WA (16°39′S, 125°29′E)	Kuzmin *et al*. (2009)
		Minah Creek, WA (17°06′S, 125°21′E)	Kuzmin *et al*. (2009)
C. beveridgei sp. nov.	*El. dentata*	Daly River, NT (13°44′S, 130°41′E)	present study
C. sprenti sp. nov.	*El. latisternum*	Wenlock Billabong, QLD (13°05′S, 142°56′E)	present study
		Hann River Roadhouse, QLD (15°11′S, 143°52′E)	present study
		Lake Tinaroo, QLD (17°15′S, 145°35′E)	present study
		Cobbold Gorge, QLD (18°48′S, 143°23′E)	present study
		Einasleigh River, QLD (18°30′S, 144°06′E)	present study
	Em. krefftii	Hann River Roadhouse, QLD (15°11′S, 143°52′E)	present study

lar to *C. tuckeri* due to inflated lips of the vulva in females and in the similar spicule length found in males (Table I). The new species differs from *C. tuckeri* in the relatively shorter distance from the anterior end of the body to the posterior end of the oesophagus, both in males (10.4–11.4% of body length in *C. sprenti* sp. nov. *vs* 13.1–15.0% in *C. tuckeri*) and females (6.7–7.5% in *C. sprenti* sp. nov. *vs* 9.8–11.9% in *C. tuckeri*). The two species also differ in host specificity and distribution: *C. sprenti* sp. nov. was found in *El. latisternum* and *Em. krefftii* in northern Queensland, whereas *C. tuckeri* occurs in *Ch. burrungandjii* and *Em. australis* in Western Australia (Table II, Fig. 35). *Camallanus sprenti* sp. nov. differs from *C. beveridgei* sp. nov. in having both lips of vulva enlarged (only the anterior lip is enlarged in *C. beveridgei* sp. nov.) and in the shape of the median ridge in the buccal capsule, which is not divided into 2 parts (tooth-like anterior and longer posterior) in *C. sprenti* sp. nov. The anterior pair of caudal papillae in *C. sprenti* sp. nov. is situated at the level of the genital alae elevation, whereas in *C. beveridgei* sp. nov. the anterior papillae are posterior to the elevation. *Camallanus sprenti* sp. nov. differs from *C. nithoggi*

and *C. waelhreow* in having shorter spicules in males: the right spicule is 345–392 long in *C. sprenti* sp. nov. *vs* 451–522 in *C. nithoggi* and 484–542 in *C. waelhreow*. The new species also has both anterior and posterior vulvar lips instead of a single anterior lip in *C. nithoggi* and no lips in *C. waelhreow*.

Pairwise sequence comparison of about 500 bp fragments at the 5' end of the 28S nuclear ribosomal DNA gene of *Camallanus sprenti* sp. nov. and 4 other known species of *Camallanus* from Australian turtles strongly supported the status of *C. sprenti* as a new species. The level of differences was substantial, from 16 bases (3.1%) between *C. sprenti* sp. nov. and *C. tuckeri* to 59 bases (11.5%) between *C. sprenti* sp. nov. and *C. waelhreow* (Table III). No intraspecific variability was detected in the sequenced fragment in 4 *Camallanus* species for which we obtained more than one sequence.

Camallanus waelhreow Rigby et Sharma, 2008

This species was originally described from *Em. krefftii*, *Em. macquarii* and *Em. macquarii dharra* from Queensland (Rigby *et al*. 2008). According to our data, it is widely distributed in Queensland and also occurs in New South Wales (see Table II). We report *Ch. expansa* as a new host record of *C. waelhreow*. The prevalence of infection in *Ch. expansa* (22%) was lower than that in *Emydura* spp.; namely *Em. macquarii* (36%, our data), *Em. krefftii* (75%), *Em. macquarii* (100%) and *Em. macquarii dharra* (72.7%), the latter three numbers from Rigby *et al*. (2008).

Camallanus nithoggi Rigby et Sharma, 2008

The species was originally described from *El. latisternum* in northern Queensland (Rigby *et al*. 2008). We found it in the same host, not far from the type locality (Table II).

Camallanus tuckeri Kuzmin, Tkach, Snyder et Maier, 2009

Originally described from *Em. australis* and *Ch. burrungandjii* in WA. Similar to *C. waelhreow*, the species was more abundant in *Emydura* than in *Chelodina*, with a prevalence 32% and 18%, respectively (Kuzmin *et al*. 2009).

Key to *Camallanus* spp. from Australian turtles

1 (2) In females, both lips of vulva indistinct, with no elevation of body wall near vulva. Parasitic in *Em. krefftii*, *Em. macquarii*, *Em. m. dharra* in New South Wales and Queensland ..... *Camallanus waelhreow* Rigby et Sharma, 2008

2 (1) In females, elevation of body wall near vulva present in the shape of vulva lip(s)

3 (6) Elevation of body wall present only anterior to vulva

4 (5) Median ridge in buccal capsule interrupted, consisting of short, tooth-like anterior part and longer posterior part. In males, anterior pair of preanal caudal papillae situated posterior to elevation of genital alae. Parasitic in *El. dentata* in Northern Territory .....*Camallanus beveridgei* sp. nov.

5 (4) Median ridge of buccal capsule usually complete, not separated into anterior and posterior portions. In males, anterior part of preanal caudal papillae situated at level of elevation of genital alae. Parasitic in *El. latisternum* in Queensland …..... *Camallanus nithoggi* Rigby et Sharma, 2008

6 (3) Elevation of body wall present both anterior and posterior to vulva in shape of two vulva lips. Anterior lip larger than posterior one.

7 (8) Distance from anterior end of body to posterior end of oesophagus about 13.1–15.0% of body length in males and 9.8–11.9% in females. Parasitic in *Em. australis* and *Ch. burrungandjii* in Western Australia .... *Camallanus tuckeri* Kuzmin, Tkach et Snyder, 2009

8 (7) Distance from anterior end of body to posterior end of oesophagus about 10.4–11.4% of body length in males and 6.7–7.5% in females. Parasitic in *El. latisternum* and *Em. krefftii* in northern Queensland ..... *Camallanus sprenti* sp. nov.

Molecular data

No intraspecific variability was observed among sequences of 3 specimens of *C. sprenti* sp. nov., 6 specimens of *C. tuckeri* and 7 specimens of *C. waelhreow* collected from different localities that were in some cases quite distant from one another (Table II; also see Kuzmin *et al*. 2009). For example, sequenced specimens of *C. sprenti* sp. nov. were collected from localities situated at a distance of up to 580 km from each other.

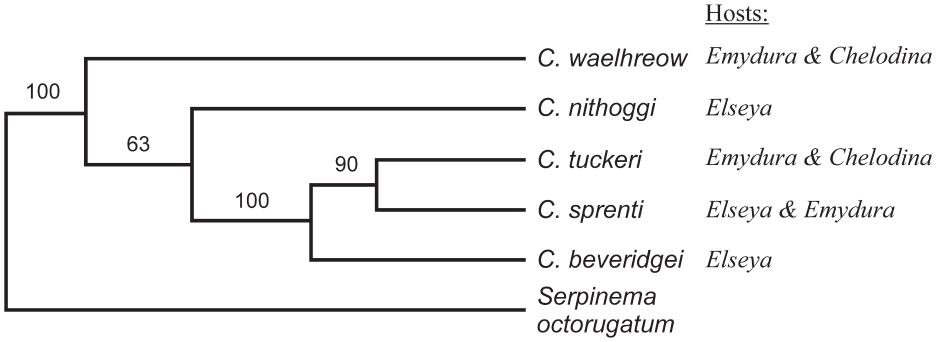


Fig. 36. Phylogenetic tree of 5 *Camallanus* species from freshwater turtles in Australia

Table III. Number (above diagonal) and percentage (below diagonal) of variable sites with the percentage based on pairwise comparison of the sequenced fragment at 5' end of 28S nuclear ribosomal DNA gene among all known species of *Camallanus* from Australian turtles. The length of the fragment was 502 bp in *C. nithoggi*, 507 bp in *C. waelhreow*, 508 bp in *C. sprenti* sp. nov., 509 bp in *C. tuckeri* and 510 bp in *C. beveridgei* sp. nov.

Species	*C. nithoggi*	*C. waelhreow*	*C. sprenti* sp. nov.	*C. tuckeri*	*C. beveridgei* sp. nov.
C. nithoggi	–	48	49	58	55
C. waelhreow	9.4%	–	59	63	60
C. sprenti sp. nov.	9.6%	11.5%	–	16	23
C. tuckeri	11.4%	12.2%	3.1%	–	29
C. beveridgei sp. nov.	10.8%	11.6%	4.5%	5.7%	–

The fragment of 28S gene used for species comparison and phylogenetic analysis was rather uniform in length across studied species and varied from 502 bp in *C. nithoggi*, to 510 bp in *C. beveridgei* sp. nov. (Table III). Sequences of *C. tuckeri* and *C. sprenti* sp. nov. showed the least number of substitutions (16 bp or 3.1%) while the biggest differences were observed among *C. tuckeri* and *C. waelhreow* (63 bases or 12.2%). The sequence comparison confirms the status of all 5 morphologically distinguishable forms of *Camallanus* from Australian freshwater turtles as independent species.

Serpinema octorugatum was used as the outgroup in our phylogenetic analysis. *Serpinema* is the genus morphologically most similar to *Camallanus* from turtles, moreover, the majority of species of *Serpinema* were once circumscribed within *Camallanus*. The tree resulting from a maximum likelihood analysis suggested the close interrelationships (100% bootstrap support) among *C. tuckeri* and *C. sprenti* sp. nov. (Fig. 36). These two species form a strongly supported clade with *C. beveridgei* sp. nov. Interrelationships among these three species and the remaining two are less obvious with rather low bootstrap support values.

Discussion

Morphology

Camallanus spp. from Australian freshwater turtles form a morphologically homogenous group, with only a few features that can be used for effective species differentiation. The pattern of buccal capsule ridge arrangement may be generalized as one median ridge with 4–5 ridges on the dorsal and ventral sides. However, the variability in the number of ridges and the presence of incomplete ridges make difficult species differentiation based on buccal capsule morphology alone (Figs 15–34). *Camallanus beveridgei* sp. nov. differs from the other 4 Australian *Camallanus* in the shape of the median ridge that consists of a shorter, tooth-like anterior part and longer posterior part separated by a small gap. Gaps between the median ridge and the nearest submedian ridges are present in *C. tuckeri*, *C. beveridgei* sp. nov. and *C. sprenti* sp. nov., however, they are less obvious in some specimens of *C. nithoggi* and are absent in *C. waelhreow* (Figs 15–22).

The number and position of caudal papillae in males of the 5 species are also very similar. There are 7 pairs of ventrolateral pedunculate preanal papillae in the preanal region. The anteriormost pair is situated at the level of the anterior elevation of ventrolateral genital alae in all species except *C. beveridgei* sp. nov. In this species, the anterior pair of papillae is situated posterior to the elevation. In the postanal region there are two ventrolateral groups of 3 pedunculate papillae just posterior to the anal opening, with one papilla from each group supporting genital alae on each side. Posteriorly, one more pair of ventrolateral papillae is associated with the genital alae and a pair of minute lateral papillae is situated closer to tail end. The anal opening is surrounded with 4 minute subventral papillae – 2 preanal and 2 postanal; this arrangement is characteristic of all Camallaninae (Petter 1979).

Differences among species are also observed in the morphology of females, particularly, in the shape and size of the body wall elevations surrounding the vulva (vulvar lips) (Figs 9, 10). In *C. waelhreow*, no signs of such elevations are present (Rigby *et al*. 2008, our observations). In *C. nithoggi* and *C. beveridgei* sp. nov. the large elevation is present only anterior to the vulva, and the posterior lip is absent in both juvenile and gravid females (Rigby *et al*. 2008; our observations). In *C. tuckeri* and *C. sprenti* sp. nov., both lips of the vulva are present, with the anterior lip being larger than the posterior one (Kuzmin *et al*. 2009; present study).

Metric characters provide additional utility in species differentiation among Australian turtle *Camallanus*. *Camallanus beveridgei* sp. nov. and *C. sprenti* sp. nov. are characterized by the largest body lengths among the 5 species; this is especially true in females. *Camallanus waelhreow* is the smallest of the 5 species. Similarly, *C. beveridgei* sp. nov. possesses the largest buccal capsule size and the widest basal ring (Table I). Tail length both in males and females of *C. beveridgei* sp. nov. is relatively shorter than in the other 4 species (Table I). Males of *C. tuckeri* and *C. sprenti* sp. nov. possess shorter spicules (the right spicule is shorter than 400) than the other 3 species (the right spicule is longer than 420) and are very similar morphologically, however, they differ in the relative distance from the anterior end of the body to posterior end of the oesophagus as a proportion of the total body length. This proportion is significantly larger in *C. tuckeri* (Table I).

Rigby *et al*. (2008) reported differences between *C. nithoggi* and *C. waelhreow* in the exterior morphology of the buccal capsule. These differences were observed after removing the tissues overlying the buccal capsule. The external morphology of the buccal capsule in *C. beveridgei* sp.

nov., *C. sprenti* sp. nov. and *C. tuckeri* has not yet been examined.

Although morphological similarities suggest the monophyly of Australian turtle camallanids additional analysis of worms from other continents is required. Several morphological characters of *Camallanus* spp. from Australian turtles are very similar to those of *C. chelonius* Baker, 1983 described from the South African pleurodire turtle, *Pelusios sinatus*. All of these worms have similar numbers of buccal capsule ridges and similarly sized and shaped tridents. Arrangement of the buccal capsule ridges in *C. chelonius* is closer to that in *C. beveridgei* sp. nov., *C. tuckeri* and *C. sprenti* sp. nov. than in *C. waelhreow* and *C. nithoggi*. In the four former species the median ridge is separated from the submedian ridges by gaps, and the posterior portions of the submedian ridges are angled towards the median ridge. *Camallanus chelonius* possesses 6 pairs of precloacal male caudal papillae in contrast to 7 pairs in all of the Australian species. However, these numbers of papillae are not unique to the aforementioned camallanids. For instance, 6 to 7 pairs of preanal papillae were also observed in species of the genus *Serpinema* (Sharma *et al*. 2002) and in species of *Camallanus* parasitizing amphibians (Ivashkin *et al*. 1971). Baker (1983) discussed some similarities between *C. chelonius* and some species of *Serpinema*, particularly, *S. amazonicus* (Ribeiro, 1941) from the South American pleurodire turtle *Podocnemis expansa*. He pointed out similarities in the structure of the buccal capsule on which the submedian ridges in *C. chelonius* tend to form dorsal and ventral groups, a feature characteristic of *Serpinema* spp. (Yeh 1960). The same pattern exists in *Camallanus* spp. from Australian turtles and is especially obvious in *C. beveridgei* sp. nov., in which the median ridge consists of a shorter anterior part and longer posterior part. This supports the Baker's (1983) notions of the close relationships among *Camallanus* from pleurodire turtles and species of *Serpinema*.

The presence and number of vulvar lips in females of *Camallanus* spp. from Australian turtles appears to be a useful character in species differentiation. *Camallanus waelhreow* differs from other species in the absence of vulvar lips, *C. nithoggi* and C. *beveridgei* sp. nov. possess only an anterior vulvar lip, and *C. tuckeri* and *C. sprenti* sp. nov possess two vulvar lips. The same variations of perivulvar structures occur in different *Serpinema* species (Ivashkin *et al*. 1971). Two alternative situations may be hypothesized: (a) there is a common plesiomorphic condition from which other variants have evolved, and (2) these variants have evolved independently in different camallanid lineages. These hypotheses can be tested using representatives of these lineages from different geographic regions and host groups.

Distribution (Table II; Fig. 35)

Two species, *C. tuckeri* found in Western Australia and *C. beveridgei* distributed in Northern Territory, are geographically separated from other species of Australian *Camallanus*. *Camallanus waelhreow*, *C. nithoggi* and *C. sprenti* are all found in the eastern part of Australia (Queensland and New South Wales). *Camallanus waelhreow* appears to have the widest distribution, spanning over 1,800 kilometers, from 19° to 36°S in Queensland and New South Wales (Rigby *et al*. 2008, our data). *Camallanus nithoggi* is considerably more restricted in distribution, being found between 17° and 18°S (Rigby *et al*. 2008, present study), with *C. sprenti* found between 13° and 18°S in Queensland (present study).

Hosts and specificity

Camallanus species were found in 7 species of Australian freshwater turtles belonging to the genera *Chelodina*, *Emydura* and *Elseya* (Table II). Six other turtle species examined as a part of our survey, namely *Ch. canni*, *Ch. longicollis*, *Ch. rugosa*, *Em. tanybaraga*, *Em. victoriae* and *Carettochelys insculpta* were free from camallanid nematodes. *Camallanus nithoggi* and *C. beveridgei* sp. nov. seem to be specific parasites of *Elseya* (Rigby *et al*. 2008, present study). The strict host specificity of *C. beveridgei* sp. nov. is supported by the fact that it was not found in *Ch. rugosa* collected from the same locality (Daly River, NT). *Camallanus waelhreow* primarily parasitize 2 *Emydura* species, *Em. krefftii* and *Em. macquarii* but were also found in *Ch. expansa* trapped in the same locality with *Em. macquarii* (our data). *Camallanus tuckeri* and *C. sprenti* sp. nov. may also infect hosts from different genera. *Camallanus tuckeri* was found in syntopic *Em. australis* and *Ch. burrungandjii* as well as in these turtles collected from separate locations. *Camallanus sprenti* sp. nov. was collected from *El. latisternum* and *Em. krefftii* occurring in the same localities, however, the prevalence was significantly higher in *El. latisternum*, than in *Em. krefftii* (73 *vs* 11%). Presumably, *El. latisternum* is a preferable host for this nematode species. As a rule *Camallanus* spp. in Australia are found more frequently and in larger numbers in species of *Emydura* and *Elseya* than they are in species of *Chelodina*. Whether this apparent preference is a product of ecological interaction or evolutionary processes is not yet clear.

Molecular phylogeny

Phylogenetic tree topology (Fig. 36) provides some insight into the trends of morphological character evolution among *Camallanus* of Australian freshwater turtles. Two species, *C. tuckeri* and *C. sprenti* sp. nov., form a well supported monophyletic group with *C. beveridgei* sp. nov. as the sister taxon. This topology is also well supported by morphological data. *C. tuckeri* and *C. sprenti* are morphologically the most similar among all 5 species examined as part of this study. They share such characters as relatively short spicules and the presence of two vulvar lips. On the other hand, *C. tuckeri*, *C. sprenti* sp. nov. and *C. beveridgei* sp. nov. do not share obvious morphological similarities, but, dorsal and ventral buccal capsule ridges in these species are more angled to the

longitudinal axis of body (Figs 25–34) than in *C. nithoggi* and *C. waelhreow* (Figs 15–24). Interestingly, the clades revealed by the molecular phylogeny and at least partly supported by morphology do not correspond to the host specificity or geographic distribution mentioned above. Restriction to parasitism of *Elseya* is scattered throughout the tree (Fig. 36) as is parasitism of *Emydura* and *Chelodina*. These patterns may reflect inadequate sampling of known *Camallanus* species, the presence of additional undiscovered *Camallanus* species, or multiple instances of host switching during the evolutionary history of this genus in Australia.

Camallanus tuckeri and *C. sprenti* sp. nov. are the most closely related phylogenetically but most distantly distributed geographically (Fig. 35). *Camallanus tuckeri* occurs in northern Western Australia while *C. sprenti* is known only in northern Queensland. The monophyletic group *C. beveridgei* sp. nov. + *C. tuckeri* + *C. sprenti* sp. nov. may be considered as a "northern" group of species while *Camallanus nithoggi* and *C. waelhreow* occur only along the east coast of Australia. Unfortunately, data on the turtle parasites from the large area between the Cape York peninsula of Queensland and eastern Northern Territory are currently lacking. Worms from this area along the Gulf of Carpentaria might reveal the extent of geographical overlap among the species concerned.

A number of fascinating questions are raised but not answered by the present study. It is unclear if the *Camallanus* of Australian turtles form a monophyletic group with *C. chelonius* from African turtles, nor is the validity of the separation of the majority of turtle camallanids into *Serpinema*. Additionally, it is not clear if *Camallanus* species from turtles are more closely related to *Camallanus* from fish and amphibians due to numerous host switches or to members of *Serpinema* parasitizing turtles worldwide (with the exception of Australia). The collection of additional specimens from around the globe and the utilisation of modern phylogenetic approaches will clarify the evolutionary history of the globally distributed but enigmatic group of nematodes.

Acknowledgements. We thank Dr. Tony Tucker, Dr. Nancy FitzSimmons and Ms. Maggie Snyder for collection assistance and Mr. Gordon Graham of CALM Kununurra and Dr. David Blair of James Cook University for making available laboratory space. This material is based upon work supported by the National Science Foundation under Grant Nos. NSF 0515492, 0515460 and 0132289.

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(Accepted January 07, 2011)