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A review and comparison of the nematode assemblages of the Australian golden bandicoot, Isoodon auratus, the quenda, I. fusciventer and southern brown bandicoot, I. obesulus (Peramelidae), from material held in the south Australian museum

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ABSTRACT

A total of 333 vials of nematodes collected from three species of *Isoodon* (representing three individuals of *I. auratus,* 63 of *I. fusciventer* and 92 of *I. obesulus*) held in the Australian Helminthological Collection of the South Australian Museum were examined. Nematodes were identified and the nematode assemblages of the three hosts were compared with each other and with the assemblage of *Isoodon macrourus.* Two fully identified species were recovered from *I. auratus,* eight from *I. fusciventer* and 14 from *I. obesulus.* None of the species occurred in all three hosts; *Labiobulura inglisi* (Subuluridae), *Peramelistrongylus skedastos* (Dromaeostrongylidae) and *Asymmetracantha tasmaniensis* (Mackerrastrongylidae) all occurred in *I. fusciventer* and *I. obesulus.* Only *Pe. skedastos* was also found in *I. macrourus.* Sorensen's index of similarity, 27.2 %, showed that *I. fusciventer* and *I. obesulus* did not have similar nematode communities and neither were their communities similar to that of *I. macrourus,* 17.1 % and 39.0 % respectively. *Labiobulura inglisi* and *Linstowinema inglisi* were the dominant nematodes in the assemblage of *I. fusciventer* and *La. inglisi* was dominant in *I. obesulus.* The two hosts had nematode assemblages with unique species profiles; one species of *Linstowinema* in *I. fusciventer,* three in *I. obesulus;* a species of *Physaloptera* in *I. obesulus,* none in *I. fusciventer;* four species of strongylid; *Asymmetracantha tasmaniensis* the most prevalent in *I. fusciventer, Peramelistrongylus skedastos* the most prevalent in *I.obesulus*. The size of the geographic range is a probable determinant of the species richness of the nematode assemblages.

1. Introduction

The genus *Isoodon* Desmarest (Peramelidae, Gray) comprises five extant species. *Isoodon auratus* (Ramsay), the golden bandicoot, formerly widely distributed across northern Australia and the arid zone, is now sparsely distributed in the northwest Kimberley region and adjacent islands as far south as the Pilbara region in Western Australia and the Wessel Group in the Northern Territory (Baker and Gynther, 2023). *Isoodon peninsulae* Thomas, the Cape York brown bandicoot, is found only on Cape York, Queensland (Baker and Gynther, 2023). *Isoodon fusciventer* (Gray), the quenda, is found in abundance in southwestern Western Australia while *I. macrourus* (Gould) the northern brown bandicoot, is found on the east coast from Sydney north and across northern Australia. *Isoodon obesulus* (Shaw) the southern brown bandicoot is found in a highly fragmented distribution along the southern and southeastern coasts, with the subspecies *I. o. nauticus* in the Nuyts Archipelago, *I. o. affinis* in Tasmania and *I. o. obesulus* in South Australia including Kangaroo Island, Victoria, and New South Wales south of Sydney (Baker and Gynther, 2023). Originally collected as a distinct species, *Perameles fusciventer* Gray, 1841, *I. fusciventer*, the quenda, was until recently considered a subspecies, *I. o. fusciventer* (Gray), of the southern brown bandicoot (see Jackson and Groves, 2015). The quenda has now been redesignated a full species based on both the previously available morphological and recently available molecular evidence (Baker and Gynther, 2023).

Members of the genus select various habitats ranging from hummock grasslands through to woodlands and open forests and have omnivorous diets including larger or smaller proportions of insects and other

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invertebrates (Baker and Gynther, 2023).

Spratt and Beveridge (2016) recorded all the published records of nematodes from *I. auratus, I. macrourus,* and *I. obesulus* including those of *I. fuscivente*r as a subspecies within *I. obesulus* in their annotated list. Two nematode species were listed from *I. auratus*, 19 plus three incompletely identified species from *I. obesulus sensu lato* and 34 species plus 4 partially identified species from *I. macrourus.* There were no records for *I. peninsulae* (see Spratt and Beveridge, 2016) and nothing is presently known about its helminth parasites. The nematode assemblage of *I. macrourus* was recently reviewed by Smales et al. (2023a). Most of the specimens relating to these records are held in the Australian Helminthological Collection (AHC) of the South Australian Museum (SAMA) with the museum holding material from *I. auratus*, *I. fuscivente*r as *I. obesulus, I. fuscivente*r and *I. obesulus* as well as material from *I. macrourus,* some of which was labelled as from *I. obesulus*.

Of the three species of *Isoodon* examined in this study only *I. auratus* is of conservation concern, being recorded in the IUCN Red List as vulnerable with a declining adult population (Burbidge and Woinarski, 2016a). Therefore, it is unlikely that collection of golden bandicoots for parasitological survey will be carried out in the future, making it important to analyse all the available information at this time. *Isoodon fuscivente*r and *I. obesulus,* by contrast, are found in abundance across the range of preferred habitats (Baker and Gynther, 2023), and are placed in the IUCN Red List as of least concern. Because of declining populations, however, as noted in Burbidge and Woinarski (2016b), Baker and Gynther (2023) deemed both species to be at risk, particularly on the mainland in areas where habitat destruction and predation by feral animals are threats.

The aims of this project were to re-examine all the nematode material available in the AHC from *I. auratus, I. fuscivente*r and *I. obesulus,* including its subspecies, to confirm, correct or provide identifications (to at least genus), for each lot. The geographic distribution of each nematode species was confirmed, the composition of the nematode community of each of the three bandicoot species was determined and comparisons were made between the communities of *I. fuscivente*r*, I. macrourus* (see Smales et al., 2023a) and *I. obesulus,* as well as between the communities of the subspecies of *I. obesulus,* namely *Isoodon obesulus affinis, I. o. nauticus,* and *I. o. obesulus.*

Table 1
Nematodes recovered from three individuals of Isoodon auratus collected in Australia from June 30, 1905.

Nematode	Locality	AHC #	Host #	Collector
Ascaridida				
Seuratidae				
Linstowinema warringtoni Smales, 1997	–	30319	–	L. Owens
Subuluridae				
Labiobulura peramelis (Baylis, 1930;	–	33140	M 3969	–
Nematode pieces	Tennant Creek, Northern Territory	33139	M 3939	–

Table 2
Localities and numbers of 63 individuals of Isoodon fuscivente r collected from Western Australia between 1977 and 2015.

Locality	Number
Albany	1
Bakers Junction, Albany	1
Brooklyn Highway 1.5 km from Perth, Canningvale	1
Collie	3
Darlington, Perth	2
De Land Graft Road, Manjimup	1
Forestdale, near Murdoch, Perth	1
Glen Forrest, Perth	7
Jarrahdale	1
Hazelmere, Perth	1
Gooseberry Hill, Perth	3
Jandacot, Perth	1
Kalamundra, Perth	4
Kalamundra Road - Great Eastern Highway bypass, Perth	1
Lesmurdie, Perth	2
Maida Vale, Perth	1
Moonza Lodge Ipsen Street, Manjimup	1
Mundarang, Perth	1
Murdoch, Perth	6
Naval Base, Stock Road, Kwinana	1
Parkerville, Perth	4
Perth	5
Radford Road/Lake Road, Perth	1
Renford/Nicholson Road, Canningvale	1
Roleystone, Perth	7
Southern River, Perth	1
Thomas Road, Madong Reserve, Kwinana	1
No Data	3
Total	63

2. Materials and methods

2.1. Material studied

All the nematode parasites collected from the Australian bandicoots registered as *I. auratus*, *I. fuscivente*r and *I. obesulus s. l.* held in the AHC (333 vials) were examined. Collection locality data were used to separate the nematodes of *I. obesulus sensu stricto* from those of *I. fuscivente*r as well as to separate the nematodes of the three subspecies of *I. obesulus.* Information recorded in the AHC database was cross checked against the original written registers and data on the specimen labels and updated if necessary. Queensland hosts that had been incorrectly identified as *I. obesulus* were eliminated from that data set and recorded for *I. macrourus*. The resulting data sets were analysed to estimate the number of hosts and the localities from where they had been collected (Tables 1–3, Fig. 1). All the specimens were stored in 70% ethanol but the collection and fixation history of most of this material is unknown.

2.2. Identification of nematodes

Specimens were processed for microscopical examination by clearing in lactophenol as temporary wet mounts, then examined using an Olympus BH2 microscope with differential interference optics (Tokyo, Japan). Measurements (in μm unless otherwise stated) for comparative purposes were taken with the aid of an ocular micrometer. Spicules were mounted in Hoyer's medium for further study and transverse sections were prepared by hand cutting with a cataract scalpel and mounted in polyvinyl lactophenol. Species identifications were confirmed by comparisons with published diagnoses and descriptions. Classification of the Strongylida follows Beveridge et al. (2014). Ecological terminology follows Bush et al. (1997).

2.3. Analysis of communities

Sorensen's index of similarity (Magurran, 1988) was calculated to compare the nematode communities of *I. fuscivente*r and *I. obesulus, I. fuscivente*r and *I. macrourus* and *I. obesulus* and *I. macrourus.* Prevalences of infection of each of the nematode species recovered were calculated as indicators of levels of infection. Since those animals that were negative when dissected are not recorded on the AHC database, the prevalences relate only to comparison between samples of infected hosts and not to a comprehensive sample of bandicoot populations as a whole.

Table 3
Localities and numbers of 92 individuals of *Isoodon obesulus* collected in Australia between 1951 and 2022.

Host	State	Locality	Number	Total
I. o. affinis	Tasmania	Beaconsfield	1	
		Bracknell District	1	
		Dunorlan	4	
		Exeter	1	
		Falmouth	1	
		Glengarry	3	
		Gog Range	1	
		Kingston	2	
		Kingston Golf Course	4	
		Launceston	2	
		Lebrina	2	
		Maggs Mountain	2	
		Margate	2	
		Railton	1	
		Smithton	1	
		Stanley	2	
		Upper Dromedary	1	
		'Tasmania'	3	34
I. o. nauticus	South Australia	Franklin Islands	3	
	(Nuyts Archipelago)	St Francis Island	2	
		West Franklin Island	4	
		Nuyts Archipelago	1	10
I. o. obesulus	New South Wales	Bobbin Head north Tunnamurra	1	
		Lismore	1	
		Nadgee State Forest	1	
		Paddington	1	
		Sidling Swamp Timbillica State Forest	1	5
	South Australia (Kangaroo Island)	Binnowie	1	
		Cape Willoughby	1	
		Elenor Downs	1	
		Hundred of Gosse	1	
		Karatta	1	
		Parndana	2	
		Vivonne Bay	2	9
	South Australia	Adelaide Hills	1	
		Crafers	1	
		Cherry Gardens	2	
		Cox's Scrub	1	
		Loftia Park	1	
		Mount Compass	1	
		Scott Creek	2	
		Spring Mountain Conservation Park	1	
		Waitpinga	1	11
	Victoria	Anglesea	1	
		Ararat	2	
		Bunyip	1	
		Cranbourne	6	
		Gorge Forest Road	1	
		Halls Gap	1	
		Healesville	4	
		Melbourne	1	
		Monash University	1	
		Moura Reserve, Grampians	1	
		Portland	2	
		'Victoria'	2	23
Total				92

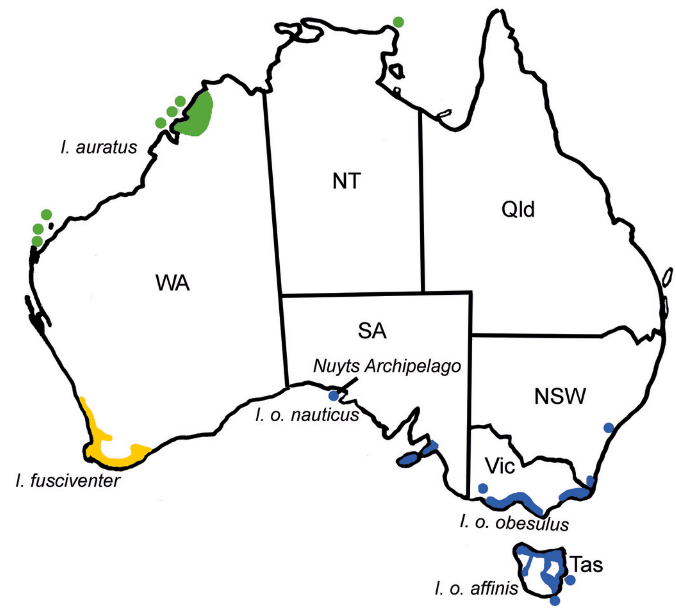

Fig. 1. Map of Australia showing the distributions of *Isoodon auratus* (green), *Isoodon fuscivente r* (yellow) and *Isoodon obesulus* (blue). Abbreviations: NT Northern Territory; NSW New South Wales; Qld Queensland; SA South Australia; Tas Tasmania; Vic Victoria; WA Western Australia. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3. Results

3.1. Identification of nematodes from I. auratus, I. fuscivente r and I. obesulus

The nematode faunas of an estimated three individuals of *I. auratus*, 63 of *I. fuscivente r* and 92 of *I. obesulus* were examined (Tables 1, 4 and 5). Fig. 1 shows the geographic distribution of the hosts examined. Two families, including two species, *Labiobulura peramelis* and *Linstowinema warringtoni* and unidentifiable fragments of nematode were recovered from *I. auratus* (Table 1). Nematodes representing nine families, including the two found in *I. auratus,* 10 genera and eight identified species were recovered from *I. fuscivente r* (Table 4) and nematodes representing 11 families, 12 genera and 14 identified species were recovered from *I. obesulus* (Table 5). For each host, nematodes that could not be identified beyond genus because either the material was damaged or only females were recovered are also listed. In the Capillariidae material that could not be identified with confidence to genus is listed as *Capillaria s. l* (see Table 6) should not be in italics. This is the reference in the text for this table.

3.2. Nematodes from I. macrourus

Nematodes from *I. macrourus* collected in Queensland, incorrectly registered as from *I. obesulus,* and not reported in Smales et al. (2023a) are listed in Supplementary Table 1. Of these, only *Strongyloides thylacis* and *Marsupostrongylus bronchialis* had not been reported previously from the SAMA AHC collection (Smales et al., 2023a).

Four lots, although recorded as from *I. obesulus* in the AHC database, have no locality data and could therefore also have been from *I. macrourus.* These nematodes registered as AHC 769, 1817, 33247 and 44930 identified as *Labiobulura peramelis, Mackerrastrongylus peramelis, La. inglisi M. isoodon* and *Capillaria s. l.* are not included in any analyses.

3.3. The nematode communities of I. fuscivente r and I. obesulus

The most prevalent species in the nematode community of *I. fuscivente r* were the ascaridids *Linstowinema inglisi* with a remarkable 100 % prevalence and *Labiobulura inglisi* with 84.1 % prevalence followed by *Asymmetracantha tasmaniensis* with 25.4 % of hosts infected. *Labiobulura inglisi,* with 66.3 %, was the most prevalent species in the nematode community of *I. obesulus* followed by *Linstowinema cinctum* 28.2 % and *Li. tasmaniense* with 20.7 % prevalence (Tables 4 and 5). *Isoodon obesulus* had the most speciose community with 14 identified

Table 4
The nematode community of 63 individuals of *Isoodon fusciventer* from Western Australia collected between 1977 and 2015.

Nematode	AHC Registration Number	Site in Host	Prevalence %
Ascaridida			
Heterakidae			
Heterakis sp.	33000	small intestine	1.6
Seuratidae			
Linstowinema inglisi (Chabaud et al., 1890)	8885, 8888, 8901, 30255–30265, 30439, 32998, 32999, 33224, 44305–07, 44906, 44918–44920, 48968–48970, 49324–49341, 49367–49383	small intestine, caecum	100
Subuluridae			
Labiobulura inglisi Mawson (1960) should be in black type, not linked; Quentin, 1969	8893, 8895, 8897, 8902, 33225–33230, 33233, 33235, 33238–33240, 44921, 49342–49357, 49384–49398	caecum, colon	84.1
La. quentini Smales, 2009	33218, 33219, 33234, 44996, 44997		7.9
Labiobulura sp.	44922		
Enoplida			
Capillariidae			
Eucoleus longiductus Spratt (2006)	32300	lips	1.6
Eucoleus sp.	49361–49366, 49413	stomach, small intestine	11.1
Capillaria sp.	47004, 47005	stomach	3.2
Capillaria s. l.	33221	small intestine	1.6
Rhabditata			
Strongyloididae			
Parastrongyloides sp.	49402	intestine	1.6
Spirurida			
Anterior piece of worm	33236	small intestine	1.6
Strongylida			
Dromaeostrongylidae			
Peramelistrongylus skedastos Mawson (1960) AS with all other authorities for species this shouls not be linked to the reference list	8894, 8903, 33004, 33005, 33220, 33222, 33231, 33232, 44936, 49405, 49410–49412	stomach	19.0
Herpetostrongylidae			
Beveridgiella sp.	8900	small intestine	1.6
Mackerrastrongylidae			
Asymmetracantha tasmaniensis Mawson (1960) see above	8898, 33002, 33003, 49400, 49404, 49406–49409, 49411, 49414–49416, 49418, 49420, 49421	small intestine, intestine	25.4
Mackerrastrongylus mawsonae Inglis, 1968	8899, 32042, 33001, 33006, 33217, 33234, 33237, 49401, 49407, 49419	intestine	15.9
Mackerrastrongylus sp.	33221, 33236, 44921, 44922, 49403, 49410, 49417	intestine	11.1
Nicollinidae			
Copemania darwini Beveridge and Durette-Desset, 2009	44921, 45393, 45394	small intestine	3.2

Table 5
The nematode community of 92 individuals of *Isoodon obesulus* collected between 1955 and 2022.

Nematode	AHC Registration Number	State	Site in Host	Prevalence %
Ascaridida				
Heterakidae				
Heterakis sp.	16488	Tas	small intestine	1.1
Seuratidae				
Linstowinema cinctum Linstow, 1898	4413, 30291–30296, 30298, 30301, 30303, 30304, 32872, 33280, 42932, 44309, 44940, 45619, 46106, 47833, 47911, 48495, 48962–48964, 49251, 49275	NSW, SA, Tas, Vic	small intestine	28.2
Linstowinema tasmaniense Smales, 1997	4458, 4530, 6929, 30300, 30302, 30305–30315, 30320, 30321, 33279	SA, Tas	small intestine	20.7
Linstowinema warringtoni Smales 1997	4446, 4460, 4461,30297, 30299, 32872	SA, Vic	small intestine	6.5
Linstowinema sp.	9162, 27967, 33274	SA, Tas, Vic	small intestine	3.3
Subuluridae				
Labiobulura inglisi Mawson (1960); Quentin, 1969 Mawson (1960) should not be linked to ref list	2929, 3317, 3343, 3346, 4781, 4895, 5375–5377, 5379, 6930, 8393, 8416, 13719, 16460, 16485, 16486, 16489, 21127, 21129, 21131, 23002, 26199, 33141–33149, 33156–33158, 33160, 33176–33181, 33196, 33197, 33246–33248, 33273, 33278, 33281, 33289, 41462, 44310, 46105, 47835, 47836, 47889,47909, 48494, 49255, 49360	Nuyts Arch., SA, Tas, Vic,	caecum, colon, small intestine	66.3
Enoplida				
Capillariidae				
Spratt (2006)Should not be linked to reference listmEucoleus parvulus Spratt (2006)	32304	Tas	small intestine	1.1
Eucoleus pseudoplumosus Spratt (2006)	32323, 32332	NSW	small intestine	2.2
Eucoleus sp.	3335, 3352, 16488, 26200, 27950,	SA, Tas	small intestine, stomach	5.4
Capillaria s. l.	33174	Tas	stomach	1.1
Trichuridae				
Baylis (1932) Should not be linked to	3336, 6928, 33159, 44916,	Tas, Vic		8.7

(*continued on next page*)

Table 5 (*continued*)

Nematode	AHC Registration Number	State	Site in Host	Prevalence %
reference listTrichuris peramelis Baylis (1932)	44939, 47834, 47838, 47890			
Rhabditata				
Strongyloididae				
Mawson (1960) Should not be linked to reference list Parastrongyloides australis Mawson (1960)	3358–3360, 41459, 46639	SA, Tas Vic		5.4
Spirurida				
Onchocercidae				
Cercopithifilaria johnstoni (Mackerras, 1954; Bain, Baker and Chabaud, 1983	33308	Tas		1.1
Physalopteridae				
Physaloptera peramelis Johnston and Mawson, 1939	33138, 33723	SA, Vic		2.2
spirurid	26196	SA		1.1
Strongylida				
Dromaeostrongylidae				
Peramelistrongylus skedastos Mawson (1960) do not linke tp ref list	3339, 3345, 3351, 3354, 8420, 8425, 16459, 16623, 26200, 32044, 33174, 33194, 33275, 33306, 44308, 47837		stomach	18.5
Herpetostrongylidae				
Beveridgiella iota (Mawson, 1960 see above) Humphery-Smith, 1980	3316, 3344, 3348, 33195, 33274, 33280, 41465, 44308, 46286	SA, Tas, Vic		9.7
Mackerrastrongylidae				
Asymmetracantha tasmaniensis Mawson (1960) see above	3334, 17276, 26196, 26200, 41460		small intestine	6.5
Mackerrastrongylus isoodon Durette-Desset and Cassone (1980) should not be linked see above	44308	Vic	small intestine	1.1
Trichostrongyloidea				
Immature worms	44308			1.1
Nematoda	16461			1.1

species compared with 8 for *I. fusciventer*. The only species to occur in both hosts were the dromeostrongylid *Peramelistrongylus skedastos* and the mackerrastrongylid *A. tasmaniensis*. Although eight genera were shared across the two hosts, the species profile for each genus differed. For example, the genus *Linstowinema* included the species *Li. cinctum, Li. tasmaniense* and *Li. warringtoni* in *I. obesulus* compared with *Li. inglisi* and *Li. quentoni* in *I. fusciventer*. Comparisons between the nematode communities of the subspecies of *I. obesulus* (Table 7) showed few differences in the species composition of their nematode communities. That only one species was collected from each of *I. o. nauticus* and *I. o. obesulus* from Kangaroo Island is likely a consequence of small host sample size rather than being an indicator of a depauperate island community.

Sorensen's indices of similarity between *I. fusciventer* and *I. macrourus, I. fusciventer* and *I. obesulus and I. obesulus* and *I. macrourus* (data for *I. macrourus* from Smales et al., 2023a), calculated using the fully identified species, were 17.1 %, 27.2 %, and 39.0 % respectively, indicating that the species composition of the three nematode communities were not similar, less than half the species being shared. The nematode community of *I. fusciventer* showed few similarities with that of either *I. obesulus* or *I. macrourus.* When genera were considered, however, the indices of 55.1 %, 72.7 % and 51.6 % respectively indicated that the generic composition of the three nematode communities had more in common. *Isoodon fusciventer* and *I. obesulus* (73 % shared genera) were the most similar and *I. obesulus* and *I. macrourus* (52 %) the least similar.

Table 6
Comparison of the nematode communities of the three sub-species of *I. obesulus*; only fully identified species included.

	I. o. affinis	I. o. nauticus	I. o. obesulus			
			SA	Vic	KI	NSW
Ascaridida						
Heterakidae						
Heterakis sp	+					
Seuratidae						
Linstowinema cinctum	+		+	+	+	+
Li. tasmaniense	+		+	+		
Li. warringtoni	+		+			
Subluridae						
Labiobulura inglisi	+	+	+	+		
Enoplida						
Capillariidae						
Eucoleus parvulus	+					
E. pseudoplumosus						+
Eucoleus sp	+		+			
Trichuridae						
Trichuris peramelis	+			+		
Rhabditata						
Parastrongyloides australis	+		+	+		
Spirurida						
Onchocercidae						
Cercopithifilaria johnstoni	+					
Physalopteridae						
Physaloptera peramelis			+	+		
Strongylida						
Dromeostrongylidae						
Peramelistrongylus skedastos	+		+	+		
Herpetostrongylidae						
Beveridgiella iota	+		+	+		
Mackerrastrongylidae						
Asymmetracantha tasmaniensis	+		+			
Mackerrastrongylus isoodon				+		

4. Discussion

4.1. Comments on identifications

The prevalence data we present above are indicative only, as they are based on an estimate of the number of hosts collected, based on AHC database records and do not include any hosts that were negative for nematode infection. Furthermore, the recovery at necropsy of nematode species living in sites other than the gastrointestinal tract is not routinely carried out because it is difficult, time consuming and only effective in freshly killed animals. As a result, the records of *Eucoleus* identified to species are exclusively from Spratt's studies (Spratt, 2006).

A single species of *Trichuris, T. peramelis,* has been described from the bandicoots *Isoodon macrourus,* as *Perameles obesula,* by Baylis (1932) from Queensland and *I. obesulus* from Tasmania by Mawson (1960). Mawson noted that the Tasmanian specimens differed from Baylis's (1932) description in the length of the spicule (2000 compared with 1400) and the size of the eggs (53 by 28–30 compared with 65 by 30–35). The specimens from *I. obesulus* from Tasmania examined for this study also had a shorter spicule (1200) and larger eggs (52–72 by 33–36) than reported by Baylis (1932) for *I. macrourus* from Queensland.

Table 7
Comparison of the nematode communities present (+) in the Australian bandicoot genus *Isoodon*. Data from Smales et al. (2023a) and this study.

	I. fuscivente	I. macrourus	I. obesulus
Ascaridida			
Ascaridae			
Ophidascaris robertsi larvae		+	
Heterakidae			
Heterakis oweni		+	
Heterakis sp	+		+
Seuratidae			
Linstowinema cinctum		+	+
Li. inglisi	+		
Li. latens		+	
Li. maplestonei		+	
Li. tasmaniense			+
Li. warringtoni		+	+
Linstowinema sp. 1 of Smales et al. (2023		+	
Subuluridae			
Labiobulura baylisi		+	
La. inglisi	+		+
La. peramelis		+	
La. quentini	+		
Labiobulura sp		+	
Enoplida			
Capillariidae			
Capillaria sp		+	
Eucoleus longiductus	+	+	
E. parvulus	+	+	
E. pseudoplumosus		+	+
Eucoleus sp	+	+	+
Trichuridae			
Trichuris peramelis		+	+
Rhabditata			
Strongyloididae			
Parastrongyloides australis			+
Pa. peramelis		+	
Parastrongyloides sp	+	+	
Strongyloides thylacis		+	
Strongyloides sp		+	
Spirurida			
Gnathostomatidae			
Gnathostoma doloresi		+	
Gnathostoma sp		+	
Onchocercidae			
Cercopithifilaria johnstoni		+	+
C. pearsoni		+	
Sprattia spearei		+	
Physalopteridae			
Abbreviata sp. larvae		+	
Physaloptera peramelis		+	+
Ph. thalacomys		+	
Physaloptera sp. of Norman and Beveridge (1999)		+	
Physaloptera sp		+	
Strongylida			
Angiostrongylidae			
Marsupostrongylus bronchialis		+	
Trichostrongyloidea			
Dromaeostrongylidae			
Peramelistrongylus skedastos	+	+	+
Herpetostrongylidae			
Beveridgiella iota		+	+
B. pearsoni		+	
Beveridgiella sp	+	+	
Mackerrastrongylidae			
Asymmetracantha tasmaniensis	+		+
Mackerrastrongylus isoodon		+	+
M. mawsonae	+		
M. peramelis		+	
Mackerrastrongylus sp		+	
Sprattellus cassonei		+	
Nicollinidae			
Copemania darwini	+		

Nevertheless, the suggestion by Mawson (1960) that these differences were not sufficient to erect a new species is supported by data collected by Smales et al. (2023a). They measured seven males and four females from *I. macrourus* from Queensland (AHC 33184, 33190, 44924, 44927, 44928), obtaining spicule lengths of 1120–1900 and egg sizes of 47 by 30. These measurements are congruent with the measurements taken from Tasmanian specimens (Mawson, 1960; this study) and therefore support the assignment of all the material from *Isoodon* spp. to *T. peramelis.*

A single female heterakid (AHC 33000) was recovered from *I. fuscivente* and a male heterakid (AHC 16488) from *I. obesulus*. The measurements of the female; length 6.5 mm, width 221, pharynx 53 long, oesophagus 905 long, oesophagus bulb 149 long, 152 wide, vulva without obvious ornamentation, vagina directed posteriorly, tail 516 long, eggs 72.6 long, 39.6 wide could not be placed in any known species of heterakid. The male, in poor condition precluding delineation of the cephalic end, had the following measurements: length 11.5 mm, width 289, oesophagus 1900 long, tail 250 long, posterior ventral sucker diameter 132, sucker to cloaca 600, spicules short, 190 long. These measurements are not consistent with any heterakid known from mammalian hosts. More specimens with intact cephalic ends need to be examined before an identification can be determined.

A *Mackerrastrongylus* sp., three males, three females, was recovered from *I. obesulus* from Victoria (AHC 44308). The length of the spicules (161, 201, 201) indicated that these specimens were *M. isoodon,* a species previously known only from *I. macrourus* from North Queensland (Durette- Desset and Cassone, 1980).

4.2. Isoodon auratus

The vulnerable status of *I. auratus* (see Burbidge and Woinarski, 2016a) validates the reporting of the two nematode species, *Labiobulura peramelis* and *Linstowinema warringtoni* that were identified for this study even though only three host individuals were examined (Table 1). This finding supports the dominance of those two ascaridid genera in the helminth communities of all the bandicoot hosts, species of *Perameles* and *Isoodon* studied thus far (Smales et al., 2023a; 2023b; this study). Although this depauperate nematode community is likely a consequence of the small number of *I. auratus* examined, it could also be an indicator of the effects of declining population numbers and reduced geographic distribution (Baker and Gynther, 2023; Burbidge and Woinarski, 2016a). It is noteworthy that species of the two nematode genera *Labiobulura* and *Linstowinema* are the dominant species in the nematode communities of *I. fuscivente I. macrourus* and *I. obesulus.* Neither *La. peramelis* nor *Li. warringtoni* has been reported from *I. fuscivente,* whose distribution in southern Western Australia does not overlap that of *I. auratus* but *Li. warringtoni* has been recorded from *I. macrourus* and *I. obesulus* and *La. peramelis* from *I. macrourus* (Smales et al., 2023a). This commonality of species in the nematode communities of *I. auratus* and *I. macrourus* is consistent with the historical distributions of the two hosts (Smales et al., 2023a, Fig. 1). At least one of the individuals of *I. auratus* was collected from the Northern Territory (Table 1) where *I. macrourus* also occurs (Baker and Gynther, 2023). There is no information as to the collection details of the two other golden bandicoots, although given the likely collection dates (all prior to 1995) and that reintroductions onto offshore islands and the mainland are recent events (2010), they were probably wild caught, not captive hosts (Baker and Gynther, 2023).

4.3. Isoodon fuscivente

Although found in abundance in various habitats including peri urban and urban environments, both predation by red foxes and feral domestic cats together with the loss and fragmentation of habitat, have had a significant impact on the distribution of *I. fuscivente.* These pressures have caused the retraction of quenda populations from woodland and heath to natural forest habitats (Baker and Gynther, 2023). Reductions in habitat may have impacted the size and complexity of its nematode community. With only 10 genera represented (eight completely identified species) the community of *I. fusciventer* was smaller than that of *I. obesulus* (12 genera, 14 species) and much smaller than that of *I. macrourus* (16 genera, 26 completely identified species) (Table 7). Sorensen's indices of similarity, 17.1 % between *I. fusciventer* and *I. macrourus* and 27.2 % between *I. fusciventer* and *I. obesulus,* however, demonstrated the distinctive composition of the community of *I. fusciventer*. The dominant species was *Li. inglisi* with 100 % prevalence, followed by *La. inglisi* also with a high prevalence of 84.1 %. *Asymmetracantha tasmaniensis* was the next most commonly encountered with a prevalence of 25.2 %. The very high prevalences of the two ascaridids was also signalled by the very high intensities of infection recorded in some host individuals, with more than 200 specimens of *Li. inglisi* in some animals and approximately 1000 specimens of *La. inglisi* in another animal. *Linstowinema inglisi* was found only in *I. fusciventer* as was *Labiobulura quentini.* The trichostrongyloid component of the community comprised four species, *Peramelistrongylus skedastos*, *A. tasmaniensis, Mackerrastrongylus mawsonae* and *Copemania darwini,* the two latter species being unique to *I. fusciventer*. Those specimens that could be identified only as *Mackerrastrongylus* sp. (females or pieces of worm) were likely also *M. mawsonae.* The lack of representatives of lung and tissue inhabiting nematodes recorded for *I. fusciventer* may be, to some extent, an artefact of dissection protocols used by collectors which focussed mainly on the gastrointestinal tract.

4.4. *Isoodon obesulus*

Isoodon obesulus, although having a highly fragmented distribution (Baker and Gynther, 2023, Fig. 1), had the most speciose nematode community comprising 14 identified species contained within 12 genera, compared with eight identified species within 10 genera for *I. fusciventer*. Moreover, the Sorensen's index between the two communities was only 27 % similarity. In contrast to *I. fusciventer,* whose community had high prevalences of both the Seuratidae and the Subuluridae (*Li. inglisi* 100 % and *La. inglisi* 84.1 % prevalence respectively), only the Subuluridae (*La. inglisi* 66.3 % prevalence had a similarly high prevalence in the community of *I. obesulus*. The seuratid *Linstowinema cinctum* and the dromeostrongylid *Peramelistrongylus skedastos* had the next highest prevalences at 28.2 % and 18.5 % respectively. The differences in the helminth communities of the two host species are highlighted by the strongylid component. *Asymmetracantha tasmaniensis* had a prevalence of 25.4 % in *I. fusciventer* and only 6.5 % in *I. obesulus. Mackerrastrongylus mawsonae,* prevalence 15.9 % in *I. fusciventer,* was not found in *I. obesulus. Beveridgiella iota,* prevalence 9.7 % in *I. obesulus* was missing from the *I. fusciventer* nematode community.

Also unique to *I. obesulus* were the seuratid *Li. tasmaniensis* and the strongyloidid *Parastrongyloides australis.* Of the enoplids, *Eucoleus longiductus, E. parvulus* and *E. pseudoplumosus* were found in *I. obesulus* (Table 5) and only *E. longiductus* in *I. fusciventer* (Table 4). Spratt and Beveridge (2016) reported all three species, *E. longiductus, E. parvulus* and *E. pseudoplumosus* from *I. obesulus.* The collection data from Spratt (2006), however, show that all three species of *Eucoleus* were described from *I. obesulus* from New South Wales and Tasmania and *E. longiductus* was also recorded from Western Australia. This latter record is now known to be from *I. fusciventer*. The difficulties in identifying capillariids to species are such that the material identified as *Eucoleus* spp. from both host species could be either one of the listed species or one or more undescribed species. The pneumospirurid*, Metathelazia naghiensis* Spratt, 1980, a lung inhabiting species, was not found in this study, and was reported only from histological sections of lungs by Spratt (2002). The onchocercid, *Cercopithifilaria johnstoni* (Table 5), a tissue inhabiting species has been recorded previously from *I. obesulus* (see Spratt and Haycock 1988). The dromeostrongylid, *Mackerrastrongylus isoodon,* recovered from a Victorian location, is the first recording of the genus in the southern brown bandicoot. There is no simple explanation for this record. *Isoodon macrourus,* the usual host of *M. isoodon,* is not found in the collection locality, Anglesea, on the southern Victorian coast. Neither has *M. isoodon* been reported from *Perameles gunnii* (Gray) or *P. nasuta* Geoffroy*,* long nosed bandicoots, which are sympatric with *I. obesulus* along parts of Coastal Victoria (Smales et al., 2023b).

4.5. Comparison of nematode communities within *I. obesulus*

The nematode communities of the subspecies of *I. obesulus,* particularly *I. o. affinis* and *I. o. obesulus,* as seen in Table 7, show almost no differences in community composition. The small sample of *I. o. nauticus,* whilst supporting the contention that *La. inglisi* is the most prevalent species in the *I. obesulus* nematode community, is not large enough to claim that it may be the only nematode species in the community of the subspecies *I. o. nauticus*. *Isoodon o. affinis* differs from *I. o. obesulus* only in the presence of three species, all at low prevalences (1.1%), an *Heterakis* sp., *Eucoleus parvulus* and *Cercopithifilaria johnstoni.* The latter two species are difficult to detect at necropsy and at low prevalence each of the species could easily be missed. The only species unique to *I. o. obesulus* was *E. pseudoplumosus,* for which a similar explanation would apply.

4.6. Comparison of nematode communities of *Isoodon* spp.

Historically there appears to have been little or no overlap of the geographic ranges of *I. fusciventer, I. macrourus* and *I. obesulus* and, as populations have declined, even less opportunity for interaction between the components of their nematode assemblages. The known fossil records of all the extant and extinct bandicoot species show overlap of range only between the extinct *Perameles myosuros* Wagner and *P. papillon* Travouillon & Phillips with *I. fusciventer* and the extinct *P. papillon* and *P. eremiana* Spencer with *I. obesulus* (see the distribution maps of Baker and Gynther, 2023). This suggests that *Isoodon* speciation could be the result of the dissolution of east-west connectivity and gene flow during the mid- Miocene. Rix et al. (2015), however, argue that although the biogeographic barrier of the Nullabor divide was formed through the late Oligocene and the Miocene many mammal species were sufficiently vagile to cross that barrier. Quantitative phylogenetic data is needed to provide further evidence as to the possibilities of interaction between the components of the nematode assemblages of *Isoodon* spp. Insufficient information is available to comment on the nematode assemblage of *I. auratus* or to compare it with that of *I. macrourus,* although their geographic ranges overlap in the Kimberley district of Western Australia and northern parts of the Northern Territory (Baker and Gynther, 2023). *Isoodon macrourus* has the largest geographic range (along the northern and eastern coasts of Australia), the greatest climatic differences (tropical monsoon to humid subtropical) (Australian Bureau of Meteorology, 2023) and the most speciose nematode community (18 genera, 27 fully identified species) (Smales et al., 2023a). By comparison *I. fusciventer* has the smallest geographic range (southwestern Western Australia), the least varied climate (warm to hot mediterranean) (Australian Bureau of Meteorology, 2023) and the least speciose nematode community (10 genera, 8 species). *Isoodon obesulus,* having the most fragmented geographic range (the southern and southeastern coasts) and a variable climatic range (cool temperate to warm to hot mediterranean) (Australian Bureau of Meteorology, 2023) has a nematode community (12 genera, 14 species) that falls between the two other host species. These findings are consistent with analyses that demonstrate that host geographical range size is one of the major determinants of parasite species richness (Kamiya et al., 2013; Dallas et al., 2020). The differences in parasite species composition are also reflected in the Sorensen's indices of similarity with *I. fusciventer* and *I. macrourus* having the least similar communities (17.1 %). Only one species, the dromeostrongylid *Peramelistrongylus skedastos* was found in all three host species.

The most prevalent nematode taxa in species of *Isoodon* were ascaridids. Seven species of *Linstowinema* and four species of *Labiobulura* were identified and each host species has a unique fauna of nematode species (Table 7). For example, *Li. inglisi* was present only in *I. fusciventer, Li. tasmaniense* and *Li. cinctum* only in *I. obesulus* and *Li. maplestonei* and *Li. latens* only in *I. macrourus.* Most ascaridids have complex life cycles with larval stages using insects, earthworms and small vertebrates as intermediate hosts (Anderson, 2000) and all bandicoot species include a range of such items in their preferred diets (Baker and Gynther, 2023). Differences in specific dietary choices and availability of infected food items due to geographic and climatic range could be the drivers of each host's unique nematode species profile.

The differing species composition of the nematode assemblages of the three brown bandicoots, *Isoodon* spp. can be further demonstrated by the species profile of the strongylids. Of the families represented in this study, most have direct life cycles (Anderson, 2000). There is a high prevalence, 25.4%, of *Asymmetracantha tasmaniensis* in *I. fusciventer* a lower prevalence of 6.5% in *I. obesulus* and absence in *I. macrourus. Mackerrastrongylus mawsonae* is found only in *I. fusciventer* while *M. peramelis* and *M. isoodon,* with the exception of a single instance in *I. obesulus,* are found only in *I. macrourus* (Table 7). There was a greater similarity in community composition (Sorensen's indices greater than 50%) when genera were considered. The characteristic nematode fauna of all the species of the host genus was a fauna in which species of *Labiobulura* and *Linstowinema* were the most prevalent. This prevalence was emphasized in that the only nematode species recovered from *I. auratus* were one species of each genus.

5. Conclusions

Although the host sample size (three) of *I. auratus,* the golden bandicoot, was very small, it was significant that the two nematode species recovered from it were representatives of the most prevalent taxa in the nematode assemblages of the three other species of *Isoodon* (*I. fusciventer, I. macrourus, I. obesulus*), brown bandicoots, that have been studied; the ascaridid genera, *Linstowinema* and *Labiobulura. Linstowinema inglisi* in particular was the overwhelmingly dominant taxon in *I. fusciventer.* Of the other components of the brown bandicoot assemblies only the dromeostrongylid, *Peramelistrongylus skedastos,* was found in all three host species. Although *I. fusciventer* had a less speciose nematode community than *I. obesulus*, both host species supported four trichostrongyloid species. Similar dietary preferences may be one of the drivers of nematode community composition in bandicoots, but size of the geographic range resulting in varying climatic zones, likely influences species richness.

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L.R. Smales: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **J.A.L. Wood:** Data curation, Validation, Writing – review & editing. **L.A. Chisholm:** Validation, Visualization, Writing – review & editing.

Declaration of competing interest

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Appendix A. Supplementary data

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