SUTAROSTRONGYLUS JOHNSONI SP. N.
(NEMATODA: TRICHOSTRONGYLINA, HELIGMOSOMOIDEA)
FROM THE PADAMELON, THYLOGALE STIGMATICA (MARSUPIALIA)
FROM QUEENSLAND, AUSTRALIA

BEVERIDGE I.* & DURETTE-DESSET M.C.**

Summary:

A new species of heligmosomoid nematode *Sutarostrongylus johnsoni* sp. n., belonging to the sub-family Herpetostrongylinae Skrjabin & Schulz, is described from the small intestine (duodenum) of the red-legged pademelon, *Thylogale stigmatica* (Gould, 1860) (Marsupialia: Macropodidae), from north-eastern Queensland, Australia. The only other species of the genus *S. kirkpatricki* Beveridge & Durette-Desset, 1986 occurs in the related host, the red-necked pademelon, *T. thetis* (Lesson, 1827) in south-eastern Queensland. The new species differs in having longer spicules and asymmetrical spicule tips as well as the presence of a comarète which develops on the right ventral aspect of the mid-region of the body. The synopse of the new species is unusual in that the inclination of the axis of orientation changes from being oblique in the anterior part of the body to being frontal in the posterior part. The same change may occur in some species of *Austrostrongylus* Chandler, 1924. Current data suggest that species of *Sutarostrongylus* are limited to a single genus of host, *Thylogale* Gray, 1837 and support the suggestion that both nematode species exhibit morphological features which are intermediate between those occurring in Herpetostrongylinae in dasyurid marsupials and those occurring in macropodid marsupials.

KEY WORDS : *Sutarostrongylus johnsoni* sp. n., nematode, Trichostrongylina, marsupials, *Thylogale*.

Résumé : *SUTAROSTRONGYLUS JOHNSONI* N. SP. (NEMATODA: TRICHOSTRONGYLINA, HELIGMOSOMOIDEA) PARASITE DE *THYLOGALE STIGMATICA* (MARSUPIALIA) AU QUEENSLAND, AUSTRALIE

Description de *Sutarostrongylus johnsoni* n. sp. (Herpetostrongylinae Skrjabin & Schulz, 1937), parasite de l'intestin grêle (duodénum) de *Thylogale stigmatica* (Gould, 1860) (Marsupialia: Macropodidae) originaire du Nord-Est du Queensland, Australie. La seule autre espèce du genre, *S. kirkpatricki* Beveridge & Durette-Desset, 1986 parasite un hôte proche, *T. thetis* (Lesson, 1827) dans le Sud-Est du Queensland. La nouvelle espèce se différencie par des spicules plus longs, des pointes spiculaires asymétriques et par une comarète ventrale droite présente dans la partie médiane du corps. Le synopse de la nouvelle espèce est original du fait que l'inclinaison de l'axe d'orientation varie le long du corps, d'oblique dans la partie antérieure à frontal dans la partie postérieure. Le même changement pourrait exister chez quelques espèces du genre *Austrostrongylus* Chandler, 1924. Des données récentes suggèrent que le spectre d'hôte de *Sutarostrongylus* est limité au seul genre *Thylogale* Gray, 1837 ce qui conforte l'idée selon laquelle, d'un point de vue morphologique, les espèces du genre *Sutarostrongylus* sont intermédiaires entre celles des genres parasites de Dasyuridae et celles parasites de Macropodidae.

MOTS CLÉS : *Sutarostrongylus johnsoni* n. sp., nématode, Trichostrongylina, Heligmosomoidea, marsupial, *Thylogale*.

INTRODUCTION

Heligmosomoid nematodes of the sub-family Herpetostrongylinae Skrjabin & Schulz, 1937 are common parasites of the upper small intestine of many Australian marsupials, some of them causing disease in their hosts (Spratt *et al.*, 1991; Beveridge & Spratt, 1996). Dasyurid marsupials (Dasyuridae), numbats (Myrmecobiidae) and various species of bandicoots (Peramelidae) are parasitised by species of the related genera *Beveridgeiella* Humphery-Smith, 1981,

Dessetostrongylus Humphery-Smith, 1981, *Patricialina* Inglis, 1968 and *Woolleya* Mawson, 1973, while the herbivorous marsupials, the possums (Petauridae, Phalangeridae) and kangaroos (Hypsipymnodontidae, Potoroidae, Macropodidae) are parasitised by three related genera, *Austrostrongylus* Chandler, 1924, *Paraustrostrongylus* Mawson, 1973 and *Sutarostrongylus* Beveridge & Durette-Desset, 1986. The latter genus, *Sutarostrongylus*, is of particular interest as it appears to be most closely related to *Dessetostrongylus* in dasyurid marsupials. If this is the case, then the herpetostrongylines may not have co-specified closely with their hosts, with host switching or colonisation being a significant feature of their evolutionary history (Beveridge & Durette-Desset, 1986).

Currently only a single species of *Sutarostrongylus* is known, *S. kirkpatricki* Beveridge & Durette-Desset, 1986, parasitic in the red-necked pademelon, *Thylogale thetis* (Lesson, 1827), in south-eastern Queensland.

* Department of Veterinary Science, University of Melbourne, Veterinary Clinical Centre, Werribee, Victoria 3030, Australia.

** Muséum National d'Histoire Naturelle, Département de Systématique et Évolution, CNRS, UMR 7138, 61, rue Buffon, 75231 Paris Cedex 05, France.

Correspondence: Ian Beveridge.

Tel.: (61) 3 97 31 22 85 – Fax: (61) 3 97 31 22 63.

E-mail: i.beveridge@vet.unimelb.edu.au

Beveridge & Durette-Desset (1986) reported a second species of *Sutarostrongylus* from the red-legged pademelon, *Thylogale stigmatica* (Gould, 1860), in north-eastern Queensland, but did not name it due to the lack of sufficient material. The currently un-named species is described in this paper, based on collections of additional specimens and the phylogenetic affinities of the genus are discussed.

MATERIALS AND METHODS

Nematodes were obtained from pademelons which had been collected as road-kills and frozen prior to autopsy. Following thawing, the contents of the small intestine were washed in water and fixed in 10 % buffered formol-saline. Nematodes were subsequently removed from the content and stored in 70 % ethanol. For morphological examination, nematodes were cleared in lactophenol. Morphological terminology follows Durette-Desset & Chabaud (1981) for the bursa and Durette-Desset (1985) for the synlophe. The synlophe was studied by preparing sequential, hand-cut transverse sections of a male 3.0 mm long and a female 3.20 mm long. The synlophe in the region of the vulva was also studied in a second female. In order to facilitate description ridges are numbered, initially from left to right in the anteriormost sections of the body. Ridges which commence more posteriorly are numbered in the order in which they appear, irrespective of position. Measurements have been presented in micrometres unless otherwise stated as the range followed by the mean and number of specimens measured in parentheses. Nematode taxonomy follows Durette-Desset (1983) and Durette-Desset & Chabaud (1993). Type specimens have been deposited in the South Australian Museum, Adelaide (SAM), the Muséum national d'Histoire naturelle, Paris (MNHN) and the British Museum (Natural History), London (BMNH).

SUTAROSTRONGYLUS JOHNSONI SP. N.

Synonyms: *Sutarostrongylus* sp.: Beveridge & Durette-Desset, 1986, p. 149; Beveridge *et al.*, 1992, p. 366; Griffith *et al.*, 2000, p. 310.

Types: holotype ♂, from duodenum of *Thylogale stigmatica* (Gould, 1860), South Mission Beach, Queensland (17° 56' S, 146° 05' E), coll. P.M. Johnson, 16.viii.1998, SAM 32169; allotype ♀, SAM 32170; 27 ♂, 46 ♀, paratypes in alcohol SAM 32171, slides of mounted nematodes SAM 28482-9; 6 ♂, 6 ♀, paratypes BMNH 2002.7.29.1-12, 10 ♂, 10 ♀, paratypes MNHN 288 MQ. Additional material examined: from *Thylogale stigmatica*: 32 ♂, 85 ♀, Society Flats, Kirrama Range, Queensland (18° 09' S, 145° 37' E), SAM 32172, 32173;

one ♂, Pearamon, Queensland (17° 19' S, 145° 37' E) (SAM 8961); one ♀, Wongabel State Forest, Queensland (17° 20' S, 145° 29' E) (SAM 12355).

Etymology: the species is named after P.M. Johnson, Queensland National Parks and Wildlife Service, who collected the material used in this description, and a colleague of Dr T.H. Kirkpatrick after whom the other species in the genus is named.

Description

Small nematodes coiled ventrally 3-4 times in tight spiral; longitudinal body musculature strongly developed (Figs 2-3). Mouth opening hexagonal, with six small triangular lips; two amphids and four submedian cephalic papillae external to lips (Fig. 1C); labial papillae not seen. Buccal capsule small, sub-globular, 10-13 deep, 15-20 wide; walls prominently sclerotised, anterior parts of wall directed antero-medially (Fig. 1B); buccal capsule approximately hexagonal in transverse section (Fig. 1D). Single dorsal tooth 7-10 long and smaller, paired subventral teeth project in to buccal capsule from base (Fig. 1D). Cephalic vesicle prominent (Fig. 1B), with 5-6 particularly prominent transverse annulations towards anterior extremity. Oesophagus slender, claviform; nerve ring in mid-region of oesophagus; excretory pore in region of oesophago-intestinal junction; deirid at level of excretory pore (Fig. 1A).

Synlophe. Body with uninterrupted longitudinal ridges on dorsal and ventral surfaces, number and positions of which vary along body. In both sexes, four ridges, three left-ventral (1-3) and one right-dorsal (5), arise posterior to cephalic vesicle. Approximately 50 µm posterior to cephalic vesicle, ventral-right ridge (4) appears (Figs 2A, 3A). About 300 µm posterior to cephalic vesicle in male (Fig. 2B) and 250 µm in female (Fig. 3B), dorsal-left ridge (6) arises in left lateral field, giving total of six ridges. Anterior to oesophago-intestinal junction, second ventral-right ridge (7) arises, in right lateral field (Figs 2C, 3B). Seven ridges, five ventral, two dorsal, present at level of oesophago-intestinal junction. Ventral-right ridge enlarges posteriorly (Figs 2D, 3C) then fuses with other ventral-right ridge to form comarête, about 800 µm from anterior end in male (Fig. 2E) and 600 µm from anterior end in female (Fig. 3D). At level of mid-body, six ridges present, three left-ventral, one ventral-right comarête, one dorsal-left and one dorsal-right (Figs 2E, 3D). In posterior third of male body, dorsal and ventral ridges diminish in size and start to disappear about 800 µm anterior to bursa (Fig. 2F). About 500 µm anterior to bursa, dorsal-right ridge disappears, while quadrangular ala appears in left lateral field (Fig. 2G). Ala and two ventral ridges disappear about 50 µm anterior to bursa (Fig. 2H). In female, about 2.0 mm from anterior end (end of mid-third of body), one ventral and dorsal-left ridges disappear

Fig. 1. – *Sutaroststrongylus johnsoni* sp. n. from the pademelon, *Thylogale stigmatica*. A, anterior extremity, right, lateral view. B, cephalic vesicle, left, lateral view. C, mouth opening, en face view, showing cephalic papillae and amphids. D, optical transverse section through buccal capsule showing single dorsal and two sub-ventral teeth. E, bursa, ventral view, with numbering of papillae and rays following system of Durette-Desset (1983). F, bursa, lateral view, showing swollen dorsal lobe (dl). G, dorsal ray. H, gubernaculum, ventral view. I, gubernaculum, lateral view. J, spicules, ventral view. K, spicule tips, ventral view. L, female tail, left lateral view. Abbreviations: dl: dorsal lobe of bursa; dt: dorsal tooth; ls: left spur of spicule; rs: right spur of spicule; vt: ventral tooth. Scale bars: A, E, J, L 100 µm; B-D, F-I, K 10 µm.

(Fig. 3E). Four ridges, three ventral and one dorsal-right, remain (Fig. 3F). About 50 μm anterior to vulva, dorsal-left ridge arises (Fig. 3G). At level of posterior sphincter, three ridges remain (Fig. 3H), disappearing 300 μm anterior to tip of tail.

Ridges of unequal size; ventral-left and dorsal-right ridges most prominently developed. In female, from 300 μm posterior to oesophago-intestinal junction to second third of body, triangular sclerotised supports present in ridges (Figs 3D, 3E). In anterior region of body, ridges oriented from ventral-right towards dorsal left, with inclination of c. 35° from sagittal axis (Figs 2A, 3B). In mid-body region, fusion of two ventral-right ridges to form comarête oriented to left, modifies axis of orientation to sub-frontal, directed from right to left, except for dorsal-left ridge which is oriented from left

towards dorsal surface. In posterior third of body, with loss of dorsal-left ridge, axis of orientation becomes sub-frontal.

Male. Measurements of holotype: length 3.60 mm, maximum width 74; cephalic vesicle 67 long; oesophagus 342 long; excretory pore 268 from anterior end; spicules 345 long; gubernaculum 59 long. Measurements of paratypes: length 2.79-3.59 (3.32, $n = 10$) mm, maximum width 70-90 (82, $n = 10$); cephalic vesicle 55-70 (63, $n = 10$) long; oesophagus 350-410 (390, $n = 5$) long; nerve ring 160 ($n = 1$) from anterior end; excretory pore 240-370 (330, $n = 5$) from anterior end; deirid 330 ($n = 1$) from anterior end. Bursa very slightly asymmetrical, with left lobe marginally larger than right; dorsal lobe shorter than lateral lobes (Fig. 1E); dorsal lobe inflated in lateral views (Fig. 1F); pre-bursal

Fig. 2. – *Sutarostrogylus johnsoni* sp. n. from the pademelon, *Thylagale stigmatica*. Synlophe in transverse sections of male, paratype, 3.0 mm long with individual ridges numbered. Orientation of figures indicated in 2A. A, 180 μm from anterior end. B, 300 μm from anterior end, arrow indicating presence of additional ridge, 6. C, 40 μm anterior to oesophago-intestinal junction, arrow indicating presence of additional ridge, 7. D, 540 μm posterior to oesophago-intestinal junction. E, 1.6 mm from anterior end, approximately in middle of body. F, 770 μm anterior to bursa, arrows indicating loss of ridges 3 and 6. G, 180 μm anterior to bursa. H, 100 μm anterior to bursa. Abbreviations: a: ala; m: comarête; D: dorsal surface of nematode; f: frontal axis of synlophe; i: intestine; L: left side of nematode; l: lateral line; o: oesophagus; R: right side of nematode; s: spicules; t: testis; V: ventral aspect of nematode; x: axis of orientation of synlophe. Scale bar: 15 μm .

papillae (1) immediately anterior to bursa. Bursal rays of type 1-3-1, with rays 2 and 6 arising first from the common trunk. Rays 2, 3, slender, divergent, curved ventrally; rays 4 thicker, straight; rays 5 and 6 slender, distal extremities curved dorsally; rays 8 extremely slender, straight, arise from common trunk with rays 4-6. Dorsal ray (rays 9, 10) slender at base, dividing at mid-length into four branches; external branches (rays 9) longer than internals (rays 10), sinuous, directed posteriorly, almost reaching margin of bursa; internal branches straight, directed posteriorly, not reaching margin of bursa; internal branches subdivide soon after origin; innermost branches very short, probably the phasmids (Fig. 1G). Genital cone small, not sclerotised; papilla 0 on small conical projection; paired papillae 7 short, inconspicuous. Spicules subequal

(Fig. 1J), 320-370 (350, $n = 10$) long, with small knobbed anterior extremity and long, cylindrical, alate shafts; shafts with prominent transverse striations giving overall reticulate appearance to spicules; medially directed alae with fine transverse striations, joined in mid-line; in spicules 350 long, anterior knob-like thickening 13, calomus or handle 130, lamina 130, tips 110; width of spicule shaft 75. Spicule tips asymmetrical (Fig. 1K); left spicule with lamina which expands slightly anterior to tip then diminishes in width at tip; internal spur originates from lamina near distal extremity, almost straight, blunt-tipped, terminating just short of spicule tip; right spicule slightly shorter than left; lamina terminates, with gradual narrowing of diameter, anterior to that of left spicule; medial spur of right spicule arises anterior to level of spur on left spi-

Fig. 3. – *Sutaroststrongylus johnsoni* sp. n. from the pademelon, *Thylagale stigmatica*. Synlophe in transverse sections of female, paratype, 3.20 mm long, with individual ridges numbered. A, 75 µm from anterior end. B, 125 µm from anterior end, arrows indicating new ridges, 6 and 7. C, immediately anterior to oesophago-intestinal junction. D, 270 µm posterior to oesophago-intestinal junction. The features seen in this section are also seen in the section cut 1.6 mm from the anterior end, that is in the mid-body region. E, 2.1 mm from anterior end, arrows indicating reduction in size of ridge 6 and loss of ridges 3 and 7. F, 100 µm anterior to vulva. G, 60 µm anterior to vulva, arrow indicating re-appearance of ridge 6. H, at level of vagina vera, arrows indicate loss of ridges 1 and 2.

Abbreviations: D: dorsal surface of nematode; f: frontal axis of synlophe; i: intestine; l: lateral line; L: left side of nematode; m: comarète; R: right side of nematode; x: axis of orientation of synlophe. Scale bar: 15 µm.

cule, more sinuous, terminates at level of tip of right spicule; spicule tips embedded in complex, transparent cuticular flange, quadrangular at distal extremity in spicule pairs dissected free from the body of nematodes (Fig. 1K), joining spurs to body of spicule. Gubernaculum clearly visible in lateral views only, 55-60 (57, $n = 10$) long (Fig. 1I); in dorso-ventral views visible as semi-transparent quadrangular plate, broader posteriorly (Fig. 1H).

Female. Measurements of allotype: length 4.34 mm; maximum width 74; cephalic vesicle 67 long; oesophagus 432 long; excretory pore 288 from anterior end; vulva 492 from posterior end; vagina 34 long; vestibule anterior to vagina 82 long, posterior to vagina 15 long; sphincters 35 long; tail 134 long. Measurements of paratypes: length 3.06-4.88 (3.65, $n = 10$) mm, maximum width 60-90 (78, $n = 10$); cephalic vesicle 50-75 (60, $n = 10$) long; oesophagus 330-390 (360, $n = 5$) long; nerve ring 190 ($n = 1$) from anterior end; excretory pore 300-400 (330, $n = 5$) from anterior end; deirid 320 ($n = 1$) from anterior end. Vulva 440-600 (490, $n = 10$) from posterior end; vagina extremely short, heavily sclerotised, 30-55 (40, $n = 10$) long; didelphic (Fig. 1L); vestibule longitudinally disposed, part anterior to vagina 75-95 (85, $n = 10$), part posterior to vagina shorter, 15-25 (20, $n = 10$); sphincters 35 long, infundibula 45-80 (54, $n = 5$) long. Anterior uterine branch with 2-4 eggs (2.9, $n = 10$); posterior uterine branch with 1-2 (1.3, $n = 10$) eggs; eggs thin-shelled, ellipsoidal, 60-75 (68, $n = 10$) long by 30-50 (38, $n = 10$) wide. Tail simple, tapering, 100-120 (116, $n = 8$) long (Fig. 1L).

DISCUSSION

The nematode species described above belongs to the genus *Sutarostrongylus* Beveridge & Durette-Desset, 1986 (Heligmosomoidea: Herpetostrongylinae) as it possesses a sub-globular buccal capsule with a single dorsal and two sub-ventral teeth, a cephalic vesicle, a synlophe in the mid-body region with four ventral ridges directed towards the left and two dorsal ridges also directed towards the left, a thickened dorsal lobe of the bursa and spicules which are prominently striated. The lack of body floats distinguishes the species described above from the genus *Austrostrongylus*, while the lack of sclerotisation of the genital cone distinguishes it from *Paraustrostrongylus*. It is distinguished from the related genus *Dessetstrongylus* in having didelphic females. In the original definition of *Sutarostrongylus*, Beveridge & Durette-Desset (1986) distinguished the genus on the basis of the frontal orientation of its synlophe, a feature it shared with *Austrostrongylus* and *Paraustrostrongylus*,

but which separated it from *Dessetstrongylus* which exhibits an oblique synlophe. In the species described above, the synlophe is oblique in the anterior part of the body, becoming frontal only in the more posterior part of the body when the dorsal left ridge disappears. In *Austrostrongylus safestatus* Beveridge & Durette-Desset, 1986, a similar oblique orientation is evident at the level of the nerve ring (Beveridge & Durette-Desset, 1986, Fig. 2F), but becomes frontal by the mid-body region (Fig. 2G). The synlophe of many species of *Austrostrongylus* is known only from sections taken at the mid-body region (Mawson, 1973; Durette-Desset, 1979; Cassone, 1983; Beveridge & Durette-Desset, 1986). Consequently, a more detailed examination of their synlophes may reveal that the change in the inclination of the axis of orientation of the synlophe is a more generalised phenomenon than has been recognised to date. Re-examination of the synlophe of *S. kirkpatricki* may reveal the same change in orientation. *S. kirkpatricki* was described from only five specimens and the synlophe was described from the mid-part of the body only.

The specimens of *Sutarostrongylus* described above, although having the characteristic transversely striated spicules of the genus, differ from *S. kirkpatricki* in a number of respects. The spicules are longer (320-370 μm compared with 230-270 μm in *S. kirkpatricki*) and the spicule tips of *S. kirkpatricki* are symmetrical while those of the species described above have markedly asymmetrical tips and an internal, sinuous spur arising near the tip of each spicule (Fig. 1K). The dorsal ray differs between the two species with rays 9 directed posteriorly in the species described above compared with rays 9 directed laterally in *S. kirkpatricki*. In the description presented above, there are three pairs of branches of the dorsal ray, as is the case in *S. kirkpatricki* as well as in species of *Austrostrongylus* (Mawson, 1973, Beveridge & Durette-Desset, 1986). The numbering system of the bursal rays of Durette-Desset & Chabaud (1981) encompasses an outer pair of papillae (9) and an inner pair (10). The third pair of branches may represent the innervation of the phasmids, although it would be impossible to demonstrate this without electron microscopical studies. Consequently, the numbering of the branches of the dorsal ray adopted here follows Durette-Desset & Chabaud (1981) and Durette-Desset (1983) in principal, but the innermost and shortest branches are not numbered. Measurements of some internal features of the species described were limited by the relatively poor state of preservation of the nematodes, and this may also account for the inability to locate the ring of labial papillae.

The species also differ potentially in the presence of an additional ridge (number 7) which forms a comarête on the right ventral aspect of the middle part of the body with ridge number 4 in the species described

above, but which is apparently absent in *S. kirkpatricki*. However, the synlophe of *S. kirkpatricki* needs to be examined in greater detail to confirm this difference. Due to the observed differences, the species described above is considered new and is named after the collector of the material, Mr P.M. Johnson.

A further feature of the synlophe of *S. johnsoni* which is of interest is the quadrangular ala which forms on the right posterior field of the posterior part of the body in the male (Figs 2G, H). Two species of *Austrostrongylus*, *A. petrogale* Beveridge & Durette-Desset, 1986 and *A. safestatus* Beveridge & Durette-Desset, 1986, have a single, poorly developed body float which forms in the same position of the body and has been considered the evolutionary precursor of the paired body floats found in other species of *Austrostrongylus* (see Beveridge & Durette-Desset, 1986). If homologous, the "ala" visible in the synlophe of *S. johnsoni* may represent the precursor of the floats seen in species of *Austrostrongylus*. Therefore both the appearance of what may be a body float as well as the change in orientation of the synlophe in *S. johnsoni*, potentially provide support for the scheme of evolution of the nematodes proposed by Beveridge & Durette-Desset (1986).

S. johnsoni is apparently not a common or abundant parasite of *T. stigmatica*. Beveridge *et al.* (1992) found the nematode in 15 % of 13 *T. s. stigmatica* collected from coastal areas in north Queensland, while Griffith *et al.* (2000) found the species in 17 % of 12 *T. s. stigmatica* from the same area and in one of five *T. s. wilcoxi* collected in southern Queensland. Its high degree of host specificity is indicated by the fact that it has not been found in any other species of macropodid examined from Queensland (Beveridge *et al.* 1989, 1992, 1998; Begg *et al.*, 1995; Griffith *et al.*, 2000). *S. kirkpatricki*, by contrast, occurs only in *T. thetis* in south eastern Queensland (Beveridge & Durette-Desset, 1986; Griffith *et al.*, 2000). These two species of hosts are closely related and are capable of hybridising (Close & Bell, 1997). The third Australian species of pademelon, the red-bellied pademelon, *T. billardieri* (Desmarest, 1822), which is now limited to Tasmania (Strahan, 1995) has been examined for parasites (Spratt *et al.*, 1991; unpublished observations), but no specimens of *Sutarostrongylus* have been found. The remaining species of *Thylogale* are restricted to Papua New Guinea and surrounding islands (Flannery, 1995), but have not been examined intensively for parasites. The available evidence therefore suggest that the genus *Sutarostrongylus* is restricted to the closely related pair of pademelon species, *T. stigmatica* and *T. thetis*.

No species of *Austrostrongylus* are known from members representing the basal clades (Flannery, 1989) of the Macropodidae (*Dorcopsis* Schlegel & Mueller, 1842; *Dorcopsulus* Matschie, 1916; *Lagorchestes* Gould, 1841;

Onychogalea Gray, 1841) (Spratt *et al.*, 1991), while *A. safestatus* and *A. petrogale* occur in species of *Petrogale*, a sister group of *Thylogale*. The remaining species of *Austrostrongylus* occur in the most recent clade containing the genera *Macropus* and *Wallabia*. Thus while it is possible to argue that this progression represents a co-evolution between parasite and host, the infection of *Thylogale* by nematodes most closely associated with *Dessetostrongylus* in dasyurid marsupials suggests that the initial infection was a colonisation event. The importance of colonisation (host switching, capture) in the evolution of the Trichostrongylinea was demonstrated by Durette-Desset (1985) and is considered to be an important mode of speciation in the strongyloid nematode parasites of macropodids (Beveridge & Chilton, 2001). The observations presented by Beveridge & Durette-Desset (1986) and herein, provide evidence for an additional instance of this phenomenon in Australian marsupials.

ACKNOWLEDGEMENTS

We wish to thank Peter Johnson for collecting the animals from which this material was obtained and Dave Spratt for comments on a draft of the manuscript.

REFERENCES

- BEGG M., BEVERIDGE I., CHILTON N.B., JOHNSON P.M. & O'CALLAGHAN M.G. Parasites of the Proserpine rock wallaby, *Petrogale persephone* (Marsupialia: Macropodidae). *Australian Mammalogy*, 1995, 18, 45-53.
- BEVERIDGE I. & DURETTE-DESSET M.C. New species of *Austrostrongylus* Chandler, 1924 (Nematoda, Trichostrongyloidea), from Australian marsupials, with a redescription of *A. minutus* Johnston & Mawson, 1938, and description of a new genus, *Sutarostrongylus*. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4^{ème} sér., 1986, 8, 145-170.
- BEVERIDGE I. & CHILTON N.B. Co-evolutionary relationships between the nematode subfamily Cloacininae and its macropodid marsupial hosts *International Journal for Parasitology*, 2001, 31, 976-996.
- BEVERIDGE I., CHILTON N.B., JOHNSON P.M., SMALES L.R., SPEARE R. & SPRATT D.M. Helminth parasite communities of kangaroos and wallabies (*Macropus* spp. and *Wallabia bicolor*) from north and central Queensland. *Australian Journal of Zoology*, 1998, 46, 473-495.
- BEVERIDGE I., SPEARE R., JOHNSON P.M. & SPRATT D.M. Helminth parasite communities of macropodoid marsupials of the genera *Hypsiprymnodon*, *Aepyprymnus*, *Thylogale*, *Onychogalea* and *Dendrolagus* from Queensland. *Wildlife Research*, 1992, 19, 359-376.
- BEVERIDGE I., SPRATT D.M., CLOSE R.L., BARKER S.C. & SHARMAN G.B. Helminth parasites of rock wallabies, *Petrogale* spp.

- (Marsupialia) from Queensland. *Australian Wildlife Research*, 1989, 16, 273-287.
- BEVERIDGE I. & SPRATT D.M. The helminth fauna of Australasian marsupials: origins and evolutionary biology. *Advances in Parasitology*, 1996, 37, 135-254.
- CASSONE J. *Austrostrongylus victoriensis* n. sp. (Nematoda, Trichostrongyloidea) parasite de *Wallabia bicolor* (Marsupialia, Macropodidae). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4^{ème} sér., 1983, 5, 767-770.
- CHANDLER A.C. A new genus of trichostrongylid worms from the kangaroo. *Parasitology*, 1924, 16, 160-163.
- CLOSE R.L. & BELL J.N. Fertile hybrids in two genera of wallabies: *Petrogale* and *Thylogale*. *Journal of Heredity*, 1997, 88, 393-397.
- DESMAREST, A.G. Mammalogie ou description des espèces de mammifères. *Encyclopédie Méthodique. Par ordre des Matières*, 1822, Suppl. 2, Agasse, Paris, 542 p.
- DURETTE-DESSET, M.C. Compléments morphologiques à l'étude des genres *Austrostrongylus* Chandler, 1924, et *Paraustrostrongylus* Mawson, 1973 (Nematoda, Trichostrongyloidea). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4^{ème} sér., 1979, 1, 1023-1030.
- DURETTE-DESSET M.C. Keys to genera of the superfamily Trichostrongyloidea. CIH Keys to the Nematode parasites of Vertebrates. Commonwealth Agricultural Bureaux, Farnham Royal, 1983, pp. 1-68.
- DURETTE-DESSET M.C. Trichostrongyloid nematodes and their vertebrate hosts: reconstruction of the phylogeny of a parasitic group. *Advances in Parasitology*, 1985, 24, 239-306.
- DURETTE-DESSET M.C. & CHABAUD A.G. Nouvel essai de classification des Nématodes Trichostrongyloidea. *Annales de Parasitologie humaine et comparée*, 1981, 56, 297-312.
- DURETTE-DESSET M.C. & CHABAUD A. G. Nomenclature des Strongylida au-dessus du groupe famille. *Annales de Parasitologie humaine et comparée*, 1993, 6, 111-112.
- FLANNERY T. Phylogeny of the Macropodoidea; a study in convergence, in: Kangaroos, Wallabies and Rat-kangaroos. Grigg G., Jarman P. & Hume I. (eds), Surrey Beatty & Sons, Chipping Norton, 1989, 1-46.
- FLANNERY T. Mammals of New Guinea. Reed Books, Sydney, 1995, 568 p.
- GOULD J. A monograph of the Macropodidae, or family of kangaroos, Part 1. J. Gould, London, 1841.
- GOULD J. The Mammals of Australia. J. Gould, London, 1860.
- GRAY J.E. Description of some new or little known Mammalia, principally in the British Museum Collection. *Magazine of Natural History (new series)*, 1837, 1, 577-587.
- GRAY J.E. Contributions towards the geographical distribution of the Mammalia of Australia, with notes on some recently discovered species, in a letter addressed to the Author. Journals of two expeditions of discovery in North-West and Western Australia during the years 1837, 38 and 39, under the authority of Her Majesty's Government, vol. 2, Appendix C, pp. 387-414. T & W Boone, London, 1841.
- GRIFFITH J.E., BEVERIDGE I., CHILTON N.B. & JOHNSON P.M. Helminth communities of pademelons, *Thylogale stigmatica* and *T. thetis* from eastern Australia and Papua New Guinea. *Journal of Helminthology*, 2000, 74, 307-314.
- HUMPHERY-SMITH I. *Beveridgiella* n. gen., *Dessetostrongylus* n. gen. (Nematoda, Trichostrongyloidea) parasites de Marsupiaux australiens. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4^{ème} sér., 1981, 2, 999-1012.
- INGLIS W.G. The geographical and evolutionary relationships of Australian trichostrongyloid nematodes and their hosts. *Journal of the Linnean Society (Zoology)*, 1968, 47, 327-347.
- LESSON R.P. Manuel de Mammalogie, ou histoire naturelle des Mammifères. Roret, Paris, 1827, 442 p.
- MATSCHIE P. Die verbreitung der beuteltiere auf Neu-guinea mit einigen Benerkungen ueber ihre einteilung in untergattungen. *Mitteilungen aus dem Zoologischen Museum Berlin*, 1916, 8, 142-182.
- MAWSON P.M. Amidostomatinae (Nematoda: Trichostrongyloidea) from Australian marsupials and monotremes. *Transactions of the Royal Society of South Australia*, 1973, 97, 257-279.
- MUELLER S. & SCHLEGEL H. Over drie buideldieren uit de familie der kangoeroes. Verhandlingen over der Natuurlijke Geschiedenis der Nederladsche overzeesch bezittingen. Netherlands Government, Leiden, 1845, pp. 129-148.
- SKRJABIN K.I. & SCHULZ R.S. Gel'mintozy krupnogo rogatogo skota i evo molodnyaka. Sel'khozgiz, Moskva, 1937, 723 p.
- SPRATT D.M., BEVERIDGE I. & WALTER E.L. A catalogue of Australasian monotremes and marsupials and their recorded helminth parasites. *Records of the South Australian Museum, Monograph Series*, 1991, 1, 1-105.
- STRAHAN R. The Mammals of Australia. Reed Books, Sydney, 1995, 756 p.

Reçu le 17 octobre 2003
 Accepté le 2 janvier 2004