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ANATRICHOSOMA HAYCOCKI SP. N. (NEMATODA : TRICHURIDAE) FROM THE PARACLOACAL GLANDS OF *ANTECHINUS* SPP.

With notes on *Skrjabinocapillaria* Skarbilovitsch

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SUMMARY. *Anatrichosoma haycocki* sp. n. (Nematoda: Trichuridae) is described from the paracloacal glands of *Antechinus swainsonii* (Waterhouse, 1840) and *A. stuartii* Macleay, 1841 (Marsupialia: Dasyuridae) from Nadgee State Forest, New South Wales, Australia. Immature male and female worms occur free in the intestine. *A. haycocki* is distinguished from other species of *Anatrichosoma* by the following suite of morphological characters: small size, absence of longitudinal cuticular striations in both sexes, subterminal constriction of male tail bearing 14 minute papillae and inflation of posterior portion of mature female giving *Trichuris*-like appearance. It is also characterised by its occurrence in paracloacal glands in a genus of small carnivorous dasyurid marsupial restricted to Australia and New Guinea.
Skrjabinocapillaria rodentium Wertheim and Chabaud, 1979 is recognised as a synonym of *Anatrichosoma gerbillis* (Bernard, 1964). The genus *Skrjabinocapillaria* Skarbilovitsch, 1946 is placed as a synonym of *Capillaria* Zeder, 1800, resulting in the new combination for the type species : *C. eubursata* (Skarbilovitsch, 1946) comb. nov.
It is suggested that deep penetration of the female uterus by the male at insemination is a behavioural feature common to members of the Trichinelloidea and that the morphology of the male reproductive tract reflects the mechanisms of penetration employed by members of each genus.

Anatrichosoma haycocki sp. n. (Nematoda : Trichuridae) des glandes paracloacales d'*Antechinus* spp., et remarques sur *Skrjabinocapillaria* Skarbilovitsch.

RÉSUMÉ. *Anatrichosoma haycocki* sp. n. (Nematoda: Trichuridae) est décrit des glandes paracloacales d'*Antechinus swainsonii* (Waterhouse, 1840) et d'*A. stuartii* Macleay, 1841 (Marsupialia: Dasyuridae) de Nadgee State Forest, New South Wales, Australie. Les mâles et les femelles immatures sont libres dans l'intestin grêle. *A. haycocki* est distinct des autres espèces d'*Anatrichosoma* par l'ensemble des caractères suivants : petite taille, absence de stries cuticulaires longitudinales dans les deux sexes, présence chez le mâle d'une petite constriction sub-

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terminale et de 14 petites papilles caudales, région postérieure des femelles mûres gonflée comme chez *Trichuris ;* en outre, la localisation (glandes paracloacales) et l'hôte (petit marsupial dasyuride d'Australie et de Nouvelle-Guinée) sont particuliers.
Skrjabinocapillaria rodentium Wertheim et Chabaud, 1979 est mis en synonymie avec *Anatrichosoma gerbillis* (Bernard, 1964). L'espèce type de *Skrjabinocapillaria, S. eubursata* Skarbilovitsch, 1946, est un *Capillaria, (C. eubursata* n. comb.) et le genre *Skrjabinocapillaria* tombe en synonymie avec *Capillaria* Zeder, 1800.
La pénétration profonde du mâle dans l'utérus au moment de l'accouplement paraît être un comportement commun aux membres des Trichinelloidea ; la morphologie de l'appareil génital mâle paraît traduire les diverses modalités de pénétration existant chez les différents genres.

Introduction

Beveridge and Barker (1976) reported an undescribed nematode in histological sections of the paracloacal glands of *Antechinus stuartii* Macleay, 1841, in Victoria. Since 1978 trichinelloid nematodes have been known encapsulated in the cloacal lumen and free in the paracloacal glands of *A. swainsonii* (Waterhouse, 1840) and *A. stuartii* in southeastern New South Wales. These represent a new species of *Anatrichosoma* Smith and Chitwood, 1954, (Trichuridae), the first known from Australia and named in honour of Mr Peter Haycock, who collected most of the material.

Materials and Methods

Specimens were fixed in hot 10 % neutral buffered formalin and stored in 70 % ethanol. They were studied after clearing in lactophenol or pure glycerin. All measurements are in microns unless otherwise indicated, the range followed by the mean in parentheses. Illustrations were made with the aid of a Leitz drawing tube.

Anatrichosoma haycocki sp. n.

(pl. 1 *fig. 1-12*)

Type specimens

Holotype: Male, South Australian Museum, (Adelaide) No. V2859.

Allotype: Female, South Australian Museum, (Adelaide) No. V2860.

Paratypes: South Australian Museum (Adelaide) Nos. V2861 - V2864, 4 males; Nos. V2865-V2869, 5 females *(A. swainsonii)*. United States National Museum of Natural History (USNM) Helm. Coll. No. 76547, 2 males, 7 females *(A. swainsonii)*.

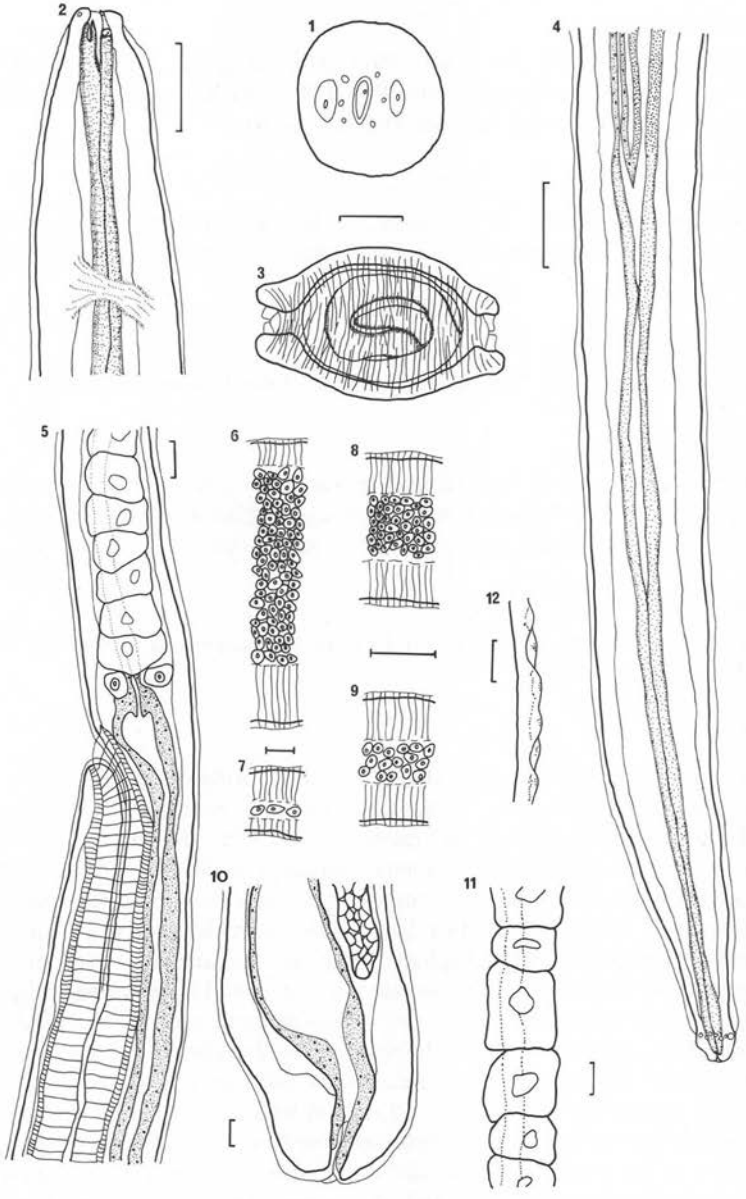

PLATE I. — *Anatrichosoma haycocki* sp. n. from *Antechinus* spp.

Fig. 1. Diagrammatic representation cephalic end, in face view, female. — Fig. 2. Cephalic end male, lateral view. — Fig. 3. Egg. — Fig. 4. Posterior end male, ventral view. — Fig. 5. Vulval region, female, lateral view. — Fig. 6. Bacillary band, female, posterior to vulva. — Fig. 7. Bacillary band male, near tail tip. — Fig. 8. Bacillary band, female, near commencement of stichosome. — Fig. 9. Bacillary band, male, near commencement of stichosome. — Fig. 10. Posterior end female, latero-ventral view. — Fig. 11. Stichocytes, mid-stichosome, male. — Fig. 12. Bacillary band, female, latero-ventral view.

Scale 0.02 mm.

Additional specimens

British Museum Coll. No. 1981. 3360-3373, 10 males, 4 females *(A. stuartii)*. Muséum national d'Histoire naturelle (Paris) No. 106 MC. bocal N438, 3 males and posterior end, 3 females and anterior end *(A. stuartii)*.

Hosts

Antechinus swainsonii (Waterhouse, 1840) and *Antechinus stuartii* Macleay, 1841 (Marsupialia: Dasyuridae); Swainson's marsupial mouse and Brown marsupial mouse.

Locality

Australia: New South Wales: Nadgee State Forest, south of Eden.

Site of infection

Mature males in epithelial lining of paracloacal glands or in connective tissue around glands, mature females free in paracloacal glands or encapsulated in lumen of cloaca. Immature males and females free in intestine.

Prevalence of infection

Found in 5 of 22 female and 3 of 17 male *A. swainsonii* and in 2 of 17 female and 0 of 4 male *A. stuartii*.

Description

Trichinelloidea (Ward, 1907), Hall, 1916, Trichuridae (Ransom, 1911), Railliet, 1915, Trichosomoidinae Hall, 1916, *Anatrichosoma* Smith and Chitwood, 1954. Small slender nematodes; males attenuated posteriorly, shorter and approximately one-quarter maximum diameter of female; mature female with *Trichuris*-like shape, narrow anterior to vulva, markedly inflated posterior to vulva; unfertilised females more uniform in width and narrow like males. Cuticle relatively thin, with fine transverse striations, without cephalic cuticular expansion, cuticular bullae or preintestinal bulge or constriction; female without dorsal hypodermal ridges. Lateral bacillary bands present in both sexes, commencing near cephalic region as narrow bands one gland cell wide, quickly broadening to 2-4 gland cells wide in male and 12-13 gland cells wide in female, terminating in tail region as narrow band of single cells in male and as broad band of 10-12 cells in female; gland cells frequently raised and noticeably dome-shaped in appearance, particularly in females; apex of dome bearing pore of gland cell. Lateral alae not observed. Cephalic extremity minute, oral opening dorso-ventrally elongated; six minute cephalic papillae around mouth, two large amphids located posterior to circle of papillae; buccal capsule small, containing large blunt dorsal stylet. Oesophagus muscular, narrow anteriorly, broadening posteriorly then narrowing again as it enters stichosome, passing through stichocytes laterally. Stichosome composed of 71-91 stichocytes, longer than wide

and regularly aligned anteriorly, wider than long and irregularly disposed posteriorly, each with large nucleus. Oesophagus approximately one-third body length in males, approximately one-seventh body length in females. Oesophago-intestinal junction with conspicuous sphincter and two conspicuous mesenchymal cells with prominent nuclei. Rectum and cloaca with modest muscular walls and thin cuticular lining; anus terminal or marginally subterminal.

Male (8 mature, in epithelial lining of paracloacal glands or in connective tissue around glands): Body 8.6-10.5 (9.6) mm long; maximum diameter 50-70 (58), diameter at nerve ring 30-40 (35), diameter at oesophago-intestinal junction 40-60 (50). Nerve ring 81-111 (98) from cephalic end. Oesophagus 3.33-3.53 (3.43) mm long, muscular portion 242-330 (272) long. Stichosome 3.06-3.26 (3.16) mm long, of 83-91 stichocytes. Cloaca 193-212 (200) long, ejaculatory duct and spicule absent. Tail with subterminal constriction surrounded by circlet of 14 small papillae.

(4 immature, free in small intestine): Body 7.9-9.7 (8.6) mm long; maximum diameter 45-50 (48), diameter at nerve ring 30, diameter at oesophago-intestinal junction 40-50 (42). Nerve ring 56-82 (68) from cephalic end. Oesophagus 1.00-3.35 (3.20) mm long, muscular portion 130-235 (178) long. Stichosome 0.83-3.17 (2.01) mm long, of 89-92 stichocytes, cells frequently longer than wide. Cloaca 125-235 (175) long, ejaculatory duct and spicule absent. Tail with inconspicuous subterminal constriction surrounded by circlet of 14 small inconspicuous papillae. Sperm present in genital tract.

Female (8 mature, encapsulated in cloaca): Body 6.4-19.9 (11.7) mm long; maximum diameter 162-310 (252), diameter at nerve ring 30-41 (36), diameter at vulva 63-100 (82). Nerve ring 51-102 (83) from cephalic end. Oesophagus 1.38-1.98 (1.70) mm long, muscular portion 200-243 (222) long. Stichosome 1.17-1.78 (1.48) mm long, of 71-85 stichocytes. Vulva 1.40-2.00 (1.72) mm from cephalic end; muscular ovejector 130-220 (172) long. Rectum 102-119 (110) long. Tail blunt, without constriction or spines.

(4 immature, free in small intestine): Body 6.7-8.9 (7.6) mm long; maximum diameter 55-70 (65), diameter at nerve ring 20-42 (32), diameter at vulva 50-59 (53). Nerve ring 24-78 (51) from cephalic end. Oesophagus 1.52-2.75 (1.87) mm long, muscular portion 80-240 (187) long. Stichosome 1.31-2.67 (1.68) mm long, of more than 72 stichocytes, cells frequently longer than wide. Vulva 1.52-1.65 (1.57) mm from cephalic end; muscular ovejector 91-246 (164) long. Rectum 36-66 (45) long. Tail blunt, without constriction or spines. Some ova present in genital tract but no sperm observed.

Egg: Bipolar, 69-79 (75) long; 44-46 (45) maximum width, 33-41 (37) minimum width, flattened in one profile, rounded in opposite giving markedly different widths depending upon orientation of egg when measuring. Egg without protruding plugs, very thick-shelled, with almost squared distal extremities. Shell with fine irregular slightly wavy transverse striations; darkly tanned. Eggs in distal uterus embryonated and containing larvae.

Discussion

Species of *Anatrichomosa* typically are found in tunnels or burrows in epithelial tissue, female worms usually in superficial layers and males frequently in the deeper tissues (Swift *et al.* 1922; Smith and Chitwood 1954; Chitwood and Smith 1958; Bernard 1964; Pence and Little 1972; Conrad and Wong 1973; File 1974; Long *et al.* 1976). They are known from mucosal epithelium of the nasal passages of Asian and African monkeys (*A. cynamolgi* Smith and Chitwood, 1954 (synonyms *A. rhina* Conrad and Wong, 1973 and *A. nacepobi* Conrad and Wong, 1973)), the stomach mucosa of *Gerbillus pyramidum* Geoffroy (*A. gerbillis* (Bernard, 1964)), the buccal mucosa of *Didelphis virginiana* Kerr (misidentified as *D. marsupialis* Linnè) (*A. buccalis* Pence and Little, 1972) and from the squamous epithelium of sclera, cornea and palpebral conjunctivae of *Tupaia glis* (Diard) (*A. ocularis* File, 1974).

A. haycocki is readily distinguished from other members of the genus by the following suite of characters: small size, presence of fine transverse cuticular striations in both sexes, subterminal constriction of the male tail bearing circlet of 14 small papillae and inflation of posterior portion of mature female giving a *Trichuris*-like appearance. These morphological characters and the occurrence of *A. haycocki* in paracloacal glands of a genus of small carnivorous dasyurid marsupial found only in Australia and New Guinea warrant erection of the new species.

In both measurements and morphological characters *A. haycocki* most closely resembles *A. ocularis*. It may be distinguished from *A. ocularis* by its greater length, longer oesophagus and stichosome (2x in males), difference in the ratio of oesophageal length: total body length (smaller in males, larger in females), greater number of stichocytes and more posterior position of vulva.

Chitwood and Smith (1958) recorded longitudinal cuticular striae in their detailed redescription of *A. cynamolgi* although Long *et al.* (1976) referred to transverse striae in the same species. All other species of *Anatrichosoma* except *A. haycocki* possess longitudinal cuticular striae. Cephalic cuticular inflations have been described in females of all species except *A. ocularis* and *A. haycocki*, and an inflated posterior portion of the female body occurs in *A. gerbillis* and *A. haycocki*. None or as many as 4 pairs of small caudal papillae have been described on the male tail of all species but no species have been reported with a caudal constriction bearing a circlet of 14 small papillae.

The cephalic structures of only *A. cynamolgi* have been studied in detail. *A. haycocki* resembles this species in the dorso-ventral elongation of the oral opening and the stylet, present in both sexes. The cephalic end differs from that of *A. cynamolgi* in having a circle of six rather than ten papillae (one cephalic papilla apparently having been lost in each quadrant), and in the exceptionally large size of the amphids.

The lateral bacillary bands in *A. haycocki* are characteristic. In the female partulicarly, bands are wide and gland cells and their pores are frequently raised and dome shaped. In this respect they resemble the structures described as 'dorsal

hypodermal ridges' posterior to the vulva in female *A. ocularis* (File, 1974) and described as 'papillae' in female *A. gerbillis* (Bernard, 1964; Pence and Little, 1972), *Trichosomoides crassicauda* (Bellingham, 1840) Railliet, 1895 and *T. nasalis* (Biocca and Aurizi, 1961). The author has studied types of *T. nasalis* and specimens from Australian rodents. The hypodermal gland cells of the lateral bacillary bands are raised and papilliform in shape and have at their apex the pore opening of the gland cell. The hypodermal ridges described and illustrated by File (1974) in *A. ocularis* probably represent a dorsal bacillary band.

Gravid females of *A. haycocki* were found free in paracloacal glands and in fibrous capsules of host origin in the lumen of the cloaca, a habitat which is not typical of congeners in which females occur in tunnels in epithelial tissue. Males recovered from the small intestine were smaller than those from paracloacal glands or subcutaneous tissue but contained sperm; however, females from the intestine were unfertilised. Presumably adult worms migrate from the intestine to their final sites and fertilisation occurs in paracloacal glands. Numerous larvated eggs were found in the waxy secretions of the glands.

Bernard (1964) described *Trichosomoides gerbillis* from the stomach of *Gerbillus pyramidum* Geoffroy in Tunisia; the species was later transferred to *Anatrichosoma* (Pence and Little, 1972).

Wertheim and Chabaud (1979) described *Skrjabinocapillaria rodentium* from the stomachs of *Meriones crassus* Sundevall, *Acomys cahirinus* (Desmarest), *Gerbillus dasyurus* (Wagner), *G. gerbillus* Olivier and *G. pyramidum* Geoffroy in Israel. From the description and illustrations it is apparent that theirs is a species of *Anatrichosoma*, and this was confirmed by examination of one male and two females from the type series. In addition, the following morphological features were observed: two small mesenchymal cells with conspicuous nuclei at the oesophago-intestinal junction, vas deferens not modified distally into a muscular ejaculatory duct, vas deferens and intestine unite and enter cloaca at same level, stichosome in females arranged irregularly in 1, 2 or 3 columns of cells, that in male arranged regularly in a single column of cells.

The specimens of Wertheim and Chabaud correspond closely in both measurements and morphology to the species described by Bernard (1964), except that the lengths of males and females from Israel are greater than those from Tunisia. Consequently, *Skrjabinocapillaria rodentium* Wertheim and Chabaud, 1979 is placed as a synonym of *Anatrichosoma gerbillis* (Bernard, 1964).

The genus *Skrjabinocapillaria* Skarbilovitsch, 1946 is characterized by the absence of a spicule and the presence of an aspinose spicular sheath or cirrus (*sensu* Rauther, 1909 as quoted in Chitwood and Chitwood, 1950). The type species of this genus, *S. eubursata* Skarbilovitsch, 1946 was originally described from unidentified bats in USSR. More recently, it has been identified in a spectrum of bat species in Poland (Zdzitowiecki, 1970), USSR (Skvortzov, 1973), Canada (Webster and Casey, 1973) and Cuba (Rutkowska, 1980).

Although unable to examine the types of *S. eubursata* the author has studied the material identified by Zdzitowiecki (1980), Webster and Casey (1973) and by

Rutkowska (1980). In addition I have seen undetermined specimens from bats in Ontario, Canada. Although difficult to observe in mature male worms because of the deeply plicated cuticular cirrus, a fine, long, non-sclerotised spicule is present in this material. The cirrus in *Capillaria* may be either spinose or aspinose. The morphological characters of *S. eubursata* are those of a *Capillaria* and I propose the new combination *C. eubursata* (Skarbilovitsch, 1946) comb. nov. Consequently the genus *Skrjabinocapillaria* falls as a synonym of *Capillaria* Zeder, 1800.

Little and Orihel (1972) described the unusual mating behaviour of *Anatrichosoma buccalis*, in which males enter the uterus of the female for up to one-half their length. In the genus *Trichosomoides* Railliet, 1895 males are permanent inhabitants of the uteri of females, and like males in the genus *Anatrichosoma* lack both spicules and a muscular ejaculatory duct. In contrast, males of the genus *Capillaria* Zeder, 1800 probably all possess a spicule and a muscular ejaculatory duct, although the spicule may be extremely difficult to observe in some species because it is weakly or non-sclerotised. In addition, the cuticle of the cloaca in all members of the genus can be everted and this structure serves as a true cirrus, functioning as a conduit for sperm. In some species of *Capillaria* e.g. *C. annulosa* (Dujardin, 1845), *C. plica* (Rudolphi, 1819) the cloaca is exceptionally long and deeply plicated in the body of the male. When fully everted a cirrus several millimeters long is formed, permitting entry deep into the uterus of the female. In the same manner, males of the genera *Trichuris* Roederer, 1761 and *Cystoopsis* Wagener, 1867 possess both a spicule and an eversible lining of the cloaca which functions as a cirrus. Male *Trichinella* Railliet, 1895 possess a vestigial spicule and a cirrus in the form of an eversible lining of the cloaca (Wu, 1955). Consequently, deep penetration of the female uterus at the time of insemination appears to be a behavioural feature common to members of the Trichinelloidea. The mechanisms of penetration employed by males are reflected in the morphology of the distal portion of the reproductive tract in each genus.

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