HISTOLOGICAL STUDY OF *TRICHOSOMOIDES NASALIS* (NEMATODA: TRICHINELLOIDEA) IN THE NASAL CAVITIES OF THE MURID *ARVICANTHIS NILOTICUS*, WITH ASSOCIATED PATHOLOGY

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Summary:

Histological study of the nasal cavities and upper maxillae of *Arvicanthis niloticus* naturally infected with *Trichosomoides nasalis* shows that the female worms reside in the epithelial monolayer of the nasal mucosa of the posterior and median cavities. Eggs laid by *T. nasalis* were infiltrated between the female body wall and the epithelial lining. Small groups of eggs, mixed with mucus and polymorphonuclear cells, were found in the nasal lumen, freed by rupture of the stretched epithelium. Two females and a few eggs were also found in the connective tissues. One male was found in a female uterus and two were apparently in the lumen of the nasal cavity but the surrounding tissues were disrupted. No male was identified in the lamina propria of the mucosa. However, significant inflammatory lesions occurred in the lamina propria, similar to those induced by the males of *Anatrichosoma* spp. which live in this part of the mucosa. In rodents, the lesions resulted in rhinosinusitis characterised by a lymphocytic infiltration leading to nasal obstruction.

KEY WORDS : *Trichosomoides nasalis*, histopathology, *Arvicanthis niloticus*.

Résumé : ÉTUDE HISTOLOGIQUE DE *TRICHOSOMOIDES NASALIS* (NEMATODA: TRICHINELLOIDEA) DANS LES CAVITÉS NASALES DU MURIDÉ *ARVICANTHIS NILOTICUS*, ET PATHOLOGIE ASSOCIÉE

*L'étude histologique des fosses nasales et du maxillaire supérieur d'*Arvicanthis niloticus *naturellement parasités par* Trichosomoides nasalis *montre que les vers femelles sont entièrement logés dans l'épithélium de la muqueuse nasale. Les œufs pondus sont infiltrés entre le corps des femelles et la fine paroi épithéliale. De petits groupes d'œufs mêlés au mucus et à des polynucléaires sont dans la lumière des fosses nasales, libérés par la rupture accidentelle de l'épithélium muqueux étiré. Quelques œufs et deux femelles ont une localisation profonde dans les tissus conjonctifs. Un mâle est dans l'utérus d'une femelle ; deux sont apparemment dans la lumière de la cavité nasale, mais les tissus avoisinants sont déplacés. Aucun mâle de* T. nasalis *n'est identifié dans le chorion de la muqueuse nasale. Cependant celui-ci est le siège de lésions inflammatoires importantes, semblables à celles induites par les mâles d'*Anatrichosoma *spp. qui vivent dans ce tissu. Chez le rongeur, ces lésions à dominante lymphocytaire réalisent une rhinosinusite responsable d'obstructions nasales.*

MOTS CLÉS : Trichosomoides nasalis, *histopathologie*, Arvicanthis niloticus.

INTRODUCTION

Parasitism of the nasal cavities of mammals by nematodes is rare and restricted to a few genera, *Nasistrongylus* Durette-Desset & Beveridge, 1981 in Trichostrongylina, *Anatrichosoma* Smith & Chitwood, 1954 and *Trichosomoides* Railliet, 1895 in Trichinelloidea (*cf.* Anderson, 2000). This location is interesting because, by inducing associated pathology (Beveridge & Barker, 1975; Allen, 1960) it may have consequences for olfaction and behaviour of the host. In this respect *Trichosomoides nasalis* Biocca & Aurizi, 1961, seems an appropriate model. Rarely reported since its discovery in Italy in *Rattus norvegicus*, this species has been recently found in Senegal in the murid *Arvicanthis niloticus* Desmarest with a high prevalence (Diagne *et al.*, 2000).

T. nasalis, as a member of Trichosomoidinae, is also interesting as this small trichinelloid subfamily displays diverse and poorly elucidated biological features (Anderson, 2000; Table I). In the present case, observations made during dissections were the only available data. The mature females of *T. nasalis* were extracted from the nasal cavities, and nearly 60 % of them housed a dwarf male in their uteri; embryonated and aborted eggs adhered to the surface of the females together with enigmatic membranous debris; no free males were recovered but an immature female 8 mm long and, when teasing a piece of ear lobe from a rodent, a larva 1.3 mm long was found (Diagne *et al.*, 2000).

The biological data reported here were obtained from a histopathological study of the nasal cavities and surrounding tissues of naturally infected rodents.

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Trichosomoidinae species	Organ	Female	Male	Laid eggs	Larva & juvenile
*Anatrichosoma cutaneum** Swift, Boots & Miller, 1922)	Skin & nasal vestibule	Multilayered epithelium	Chorion		?
*Anatrichosoma cynamolgi** Smith & Chitwood, 1954	Nasal vestibule	Multilayered epithelium	Chorion		?
Anatrichosoma sp.** Orihel, 1970	Nasal vestibule	Multilayered epithelium	?	Cutaneous tube	?
Anatrichosoma buccalis°* Pence & Little, 1972	Palate, buccal cavity	Multilayered epithelium	Chorion & lymphatic vessel		?
Anatrichosoma haycocki°°* Spratt, 1982	Paracloacal gland	Free in lumen or encapsulated	Epithelium or connective tissue		Intestinal lumen
Trichosomoides crassicauda (Bellingham, 1840)	Urinary bladder & urinary tract	Urinary epithelium	Female or ureter lumen	Urine	Blood, lungs, coelomic cavities, kidney, ureter
Trichosomoides nasalis Biocca & Aurizi, 1960	Nasal cavities median & posterior	Mucosal epithelium	Female or lumen	Mucosal secretions	?

* From Asiatic and ** African monkeys. ° From American and °° Australian marsupials. Other species are from rodents. Underlined: mating location.

Table I. – Biological characteristics of studied species of Trichosomoidinae.

MATERIAL AND METHODS

Of a total of 19 *A. niloticus*, three were trapped in the village of Bandia, close to Mbour, 60 kms south-east from Dakar, Thiès region (number 1 EC). A few eggs were found when examining their faeces which resembled those of *T. nasalis* but may also have belonged to a gastric trichosomoidine, *Anatrichosoma* sp., resembling *A. gerbillis* (Bernard, 1964), recently reported in the same region from another murid (Dr M. Diouf, personal communication). The remaining 16 *A. niloticus*, 11 adult and five juvenile specimens, were trapped at Richard Toll, along the Senegal river, the northern border between Senegal and Mauritania; faeces were not examined (number 2 EC).

The rodents were killed and fixed in toto in 10 % neutral formalin. The heads were isolated and decalcified for 24 hours (DC-LMR decalcifiant). They were cut with a razor blade into frontal slices 0.5 cm thick, across the nasal cavities and upper maxillae. The slices were embedded in paraffin, oriented parallel to the frontal plane, and 5 µm thick sections were prepared and stained with haemalum-eosin-safran. The histological sections have been deposited in the MNHN, Paris, collection numbers 022513 A1 & 2, B1 & 2, C1 & 2 for 1 EC; C3 to 19 for 2 EC.

RESULTS

T. nasalis was present in the three rodents from Bandia (A2, B2 and C2), and in two among those from Richard Toll (C7 and C18).

IDENTIFICATION OF *T. NASALIS* IN SECTIONS

Identification of the worm sections (Figs 1-3) is based on the diameter and anatomy as described by Diagne *et al.* (2000).

Mature female: cuticle thin, its transverse striations obvious when obliquely sectioned; hypodermis very thin, except at level of the lateral bacillary bands. Bacillary cells and their openings on bosses identified in several sections (Fig. 2B). Musculature extremely reduced. Anterior part: diameter 85-92 µm; stichocytes filling body cavity; each stichocyte with voluminous nucleus and large nucleolus; reduced oesophageal lumen on side of stichocytes (Figs 2A, 3H). Posterior part: diameter reaching 250 µm; uterus filling body cavity; thick wall of uterus contrasts with thin body wall of worm (Figs 1B, 3B, C & E). In uterine lumen, eggs at diverse stages of development. Few spermatozoa with bacillus-like nuclei identified in distal part of uterus. Hologonic ovary observed in sections, 160-210 µm in diameter (Figs 2B, 3D), ovogonia and ovulae seen in same transverse section.

Young female: anterior part, 45–50 µm in diameter at level of stichocytes (Fig. 1C & D). Postoesophageal section, 55 µm in diameter, through intestine and thick walled vagina (Fig. 1C).

Male: 30 µm in diameter anteriorly (Fig. 3F & G), 40-60 µm at level of testis. Hologonic testis: spermatogonia with round nuclei at periphery, spermatozoa bacillus-like with densely stained nuclei near central axis. Vas deferens with spermatozoa in lumen (Fig. 2C).

Eggs: about 80/50 µm. In uteri, mature eggs with thick shell, refringent with polarized light, whether embryonated or aborted (Figs 2E, 3C). Eggs still with thin soft shell may contain fully developed larvae (Fig. 2D). First stage larvae, 10-12 µm wide; tiny duct with refringent wall corresponding to stylet; muscular oesophagus 48 µm long; stichocytes with conspicuous nuclei and granular cytoplasm. The anatomy of the first stage larva appears similar to that described in other trichinelloids (Wehr, 1939; Morehouse, 1944; Thapar & Singh, 1954, for hatching larvae; Wright, 1961 for developing first stage larvae).

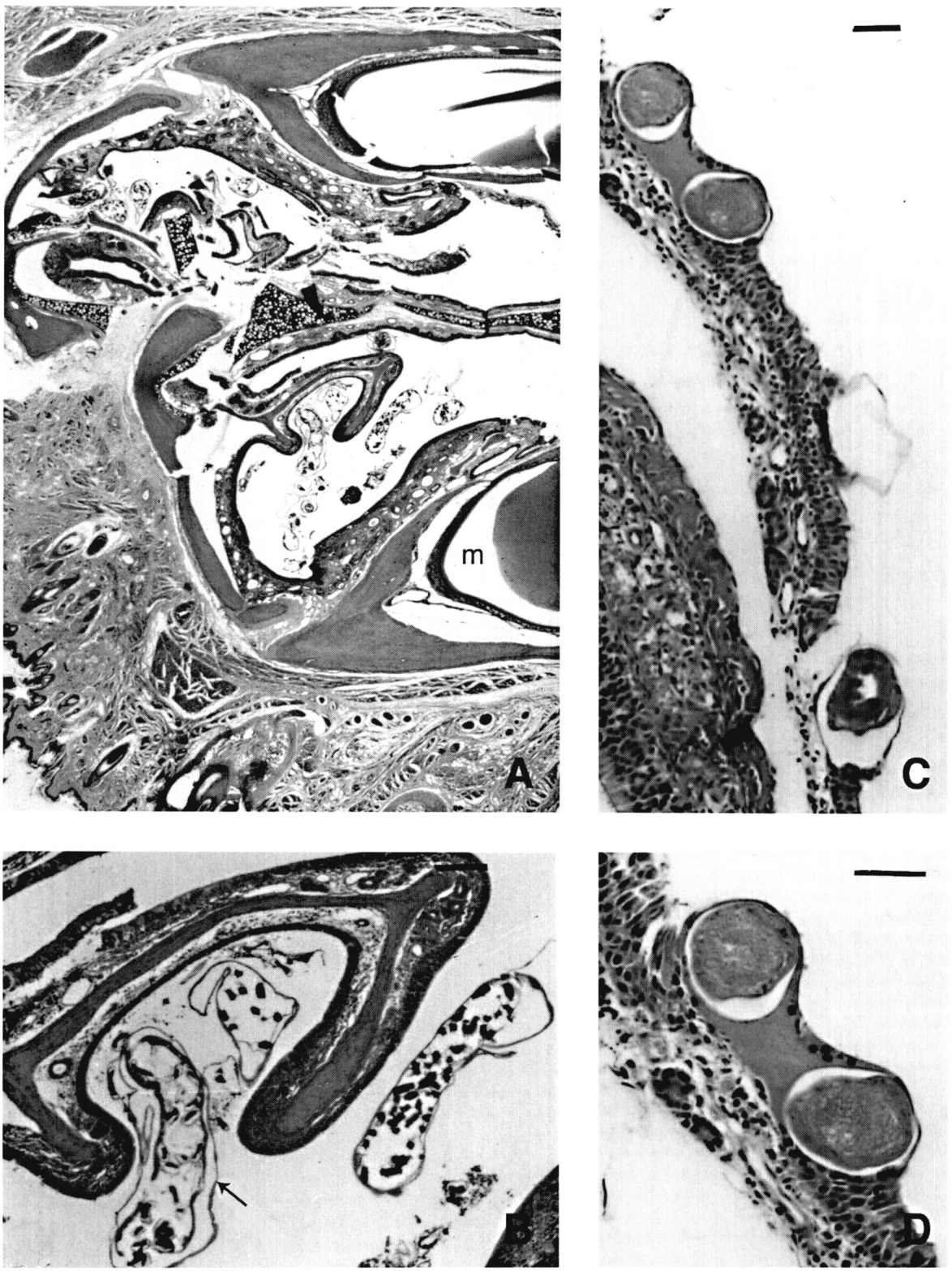

Fig. 1. – *Trichosomoides nasalis* from *Arvicanthis niloticus*. A. Posterior nasal cavities with several sections of mature females. Males are present but not identified at this low magnification (m: molar). B. Detail of a nasal septum and female posterior regions bulging into the nasal cavity; the body wall of the worms and the epithelium membrane of the mucosa form a thin envelop (arrow), the uterine wall is thicker; on right and below, eggs in mucous with inflammatory cells. C. Epithelium of the nasal mucosa with sections of a young female, at level of stichocytes (upper left), at level of the vagina and intestine (below); a section of worm has shifted and the epithelial lining remains. D. Detail of mucosa with epithelium and two female worm sections with noncellular substance in the burrowed epithelium; the lamina propria has a normal aspect. Scale bars in µm: A, 300; B, 150; C, 45; D, 40.

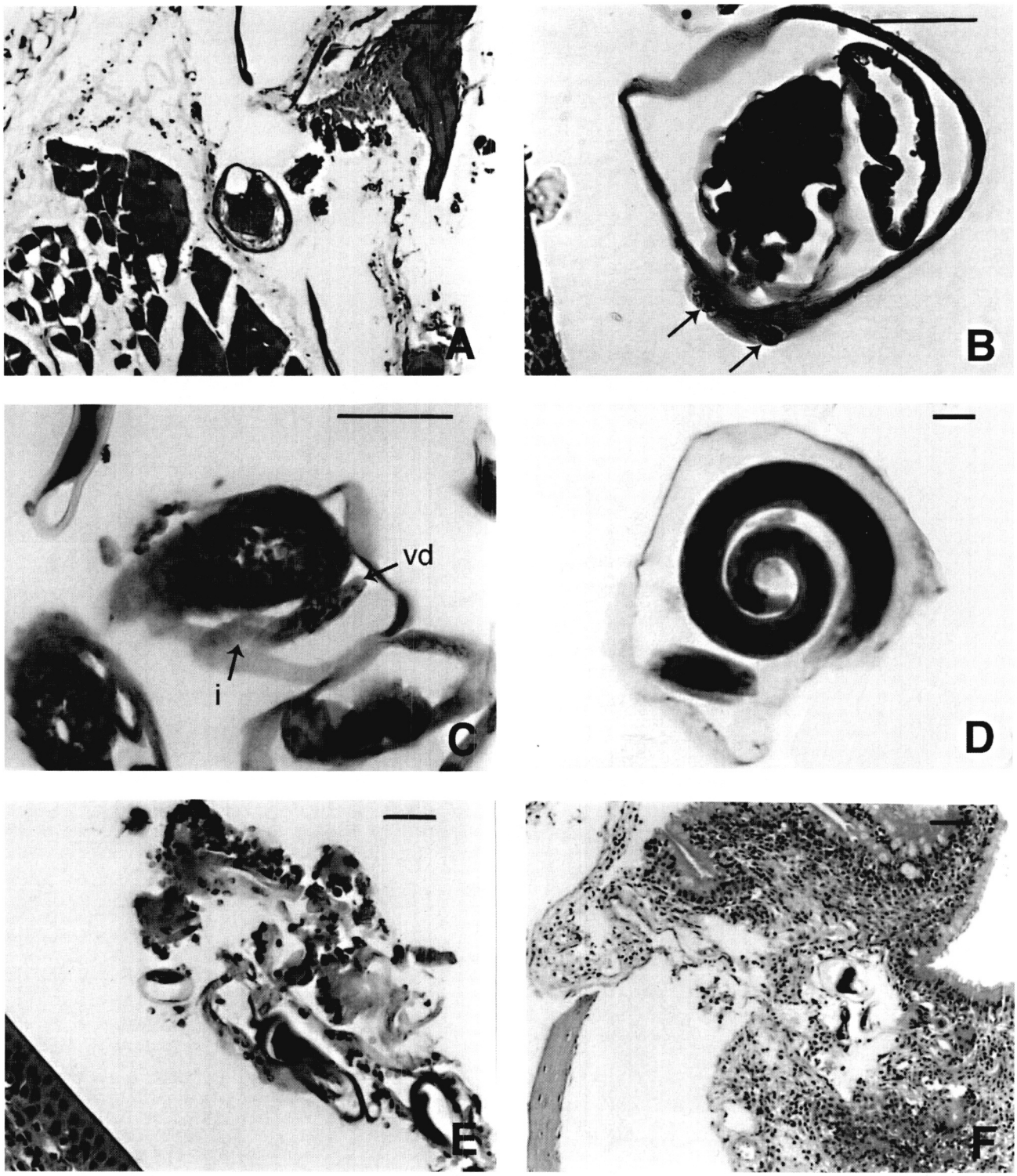

Fig. 2. – Sections of *T. nasalis* in the nasal cavities. A. Mature female at level of a stichocyte, in the connective tissue of the external aspect of the upper maxilla. B. Female, at level of ovary and intestine, with two bosses of lateral bacillary cells (arrow). C. Three sections of a male at level of testis, in nasal lumen (vd: vas deferens; i: intestine); an egg (upper left). D. Larva in egg with thin, soft shell. E. Eggs in the lumen of nasal cavity, mixed with mucus and inflammatory cells. F. Three eggs in the chorion. Scale bars in µm: A, 60; B, 65; C, 30; D, 12; E, 20; F, 60.

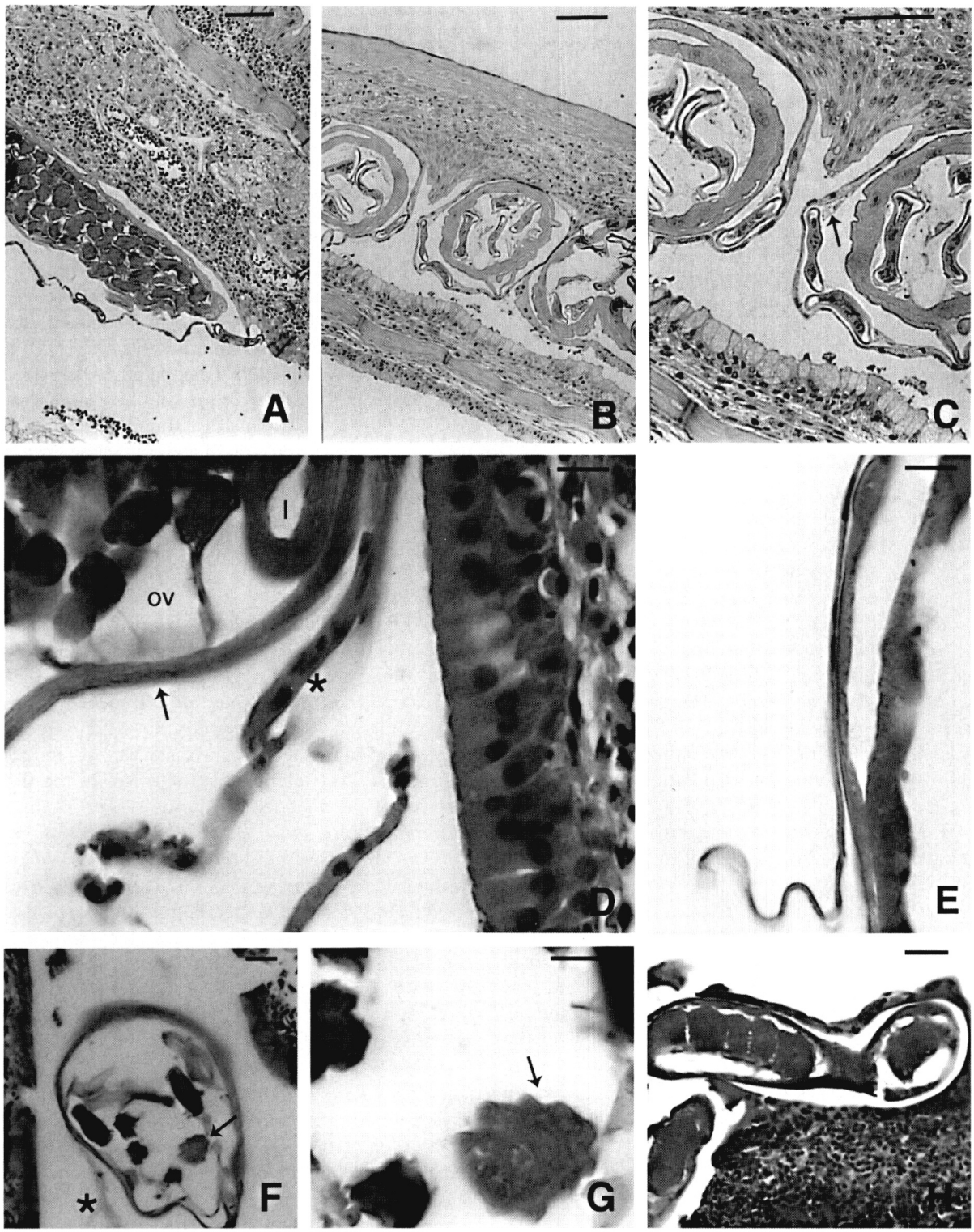

Fig. 3. – Mature females of *T. nasalis* from *A. niloticus*. A. Longitudinal section through the uterus filled with eggs, and lamina propria infiltrated by inflammatory cells, mainly lymphocytes. B. Three transverse sections of a female in the epithelium of the mucosa; below, which is nromal mucosal epithelium. C. Detail of thick uterine wall, and a few eggs laid between the worm's thin body wall (arrow) and the stretched epithelium. D. Detail of female body wall (arrow) and epithelium (*) at level of ovary (ov) and intestine (I); a few polymorphonuclear cells on the epithelial membrane (below). E. Longitudinal worm section showing, from right to left, the thick uterine wall, the body wall and the very thin mucosal epithelium. F. Transverse section through the uterus with eggs and an anterior section of a male (arrow); the epithelial membrane is identified (*). G. Detail of the section of the male (arrow); two developing eggs, on left. H. Longitudinal section at level of stichosome showing intense inflammatory infiltration in the lamina propria. Scale bars in µm: A, B, 100; C, 50; D, 12; E, 8; F, 30; G, 15; H, 45.

LOCALIZATION OF *T. NASALIS*

In sections, the three pairs of anterior, median and posterior nasal cavities are identifiable, as are the nasal septa which separate them and the upper maxillae with two molars in their alveolae (Fig. 1A). The nasal epithelium is composed of ciliated cells longer than wide and mucous cells (Figs 1C & D, 3C); its thickness and the mucous cell density vary greatly according to the location. The underlying connective tissue, the lamina propria, is rich in blood and lymphatic vessels.

Only the larger posterior region of females can be identified at first in the nasal cavities (Fig. 1A & B); a more careful examination is necessary to detect the anterior regions of females, which are less frequent and smaller (Figs 1C, 3H).

The anterior parts of female *T. nasalis* lie within the nasal epithelium; the bacillary bands are in close contact with the epithelium; sections at the level of the vagina are within the nasal epithelium (Fig. 1C); in some cases, a noncellular substance fills the intraepithelial cavity formed by the parasite (Fig. 1D). Female posterior parts appear at first to be free in the nasal cavity into which they protrude (Fig. 1A & B); they are in fact also surrounded by the nasal epithelial membrane. The considerably stretched membrane tightly adheres to the body wall of the worm; epithelial cell nuclei are flattened and sparse (Fig. 3C). The epithelial membrane is fragile and may be torn (Fig. 3D & E). A few female worm sections in the nasal cavity are not surrounded by the epithelial membrane (Fig. 2B). A section of a female, at the level of the stichocytes and 90 µm in diameter, is localized in the connnective tissue of the external aspect of the upper maxillae (Fig. 2A).

Three males were identified, all from the same rodent, one in the left posterior nasal cavity and two in the right. The first male, an anterior section, was inside a female uterus (Fig. 3F & G); the body wall of the second was close to a fragment of stretched epithelium membrane; the last lay apparently free in the nasal cavity but the surrounding tissues were disrupted (Fig. 2C).

Eggs were numerous within and outside the uteri. Many were situated between the female body wall and the expanded epithelium of the mucosa (Fig. 3B & C). Others were in the lumen of the nasal cavities, mixed with mucous and inflammatory cells (Fig. 2E). In one rodent, a few eggs were seen in the lamina propria of the mucosa (Fig. 2F).

TISSUE LESIONS

The lesions were irregularly distributed. They involved the epithelium and the chorion of the nasal mucosa. The epithelium is invaded into by the female parasites (Fig. 1C & D) but not destroyed; it forms a thin homogeneous eosinophilic membrane in which flat nuclei can be identified; the ciliated apices of the cells have disappeared as well as the mucous cells (Figs 1D, 3A-E). Small groups of inflammatory cells, mainly polymorphonuclear neutrophil cells, were infiltrated between the epithelial membrane and the cuticle of posterior parts of the worms (Fig. 3D). The lamina propria was intensely infiltrated with inflammatory cells, predominantly lymphocytes, although generally without worms in this study (Fig. 3A & H); eosinophils are present at low density. Mild polymorphonuclear cell infiltration was seen close to the few eggs in the chorion (Fig. 2F). The nasal mucus contained polymorphonuclear neutrophils and a few eosinophils. The lesions resulted in a subacute chronic rhinitis. Rhinitis was also found associated with the trichostrongylid *N. antechini* (Beveridge & Barker, 1975) which lives in the cavity and not in the epithelium; this parasite, contrary to *T. nasalis*, also induced locally squamous metaplasia or erosion of the epithelium (Beveridge & Barker, 1975).

DISCUSSION

The females of *T. nasalis* parasitize mucosal epithelium like other members of the Trichosomoidinae (Anderson, 2000), perhaps with the partial exception of *Anatrichosoma haycocki* Spratt, 1982 in which females only were described lying free in the lumen of the infected organ (Table I). The females of *T. crassicauda* (Bellingham, 1840) live in the uroepithelium of the bladder of murids (Lowenstein, 1910; Antonakopoulos *et al.*, 1991; Serakides *et al.*, 2001), those of *Anatrichosoma buccalis* Pence & Little, 1972 in the buccal epithelium of a marsupial, and those of several *Anatrichosoma* species from monkeys, *A. cutaneum* (Swift, Boots & Miller, 1922), *A. cynamolgi* Smith & Chitwood, 1954, and *Anatrichosoma* spp. *sensu* Orihel, 1970, in the epithelium of the nasal cavities or in the skin (Swift *et al.*, 1922). The mucosal epithelium is likely to be the basic habitat of the Trichinelloidea (Wright, 1989).

The species from monkeys known as nasal parasites in fact inhabit the nasal passages (Chitwood & Smith, 1958; Allen, 1960; Orihel, 1970; Long *et al.*, 1976); the female worms lie in a multilayered epithelium. *T. nasalis* was seen in the nasal cavities and females invaded a monolayered epithelium. This feature is common with other Trichinelloidea, such as *Trichinella spiralis* (Owen, 1835) (Gardiner, 1976) and *Trichuris* spp. in the intestinal epithelium. Comparison with these species sheds light on the possible relationships between *T. nasalis* and the epithelium of the mucosa: the first stage larva (Kozek 1971a, b) of *T. spiralis* penetrates an intestinal cell and burrows its way by invading and destroying the adjacent epithelial cells (Appleton,

2001); the first stage larva of *T. muris* (Schrank, 1788) induces the formation of a syncytium (Lee & Wright, 1978).

In the present study of *T. nasalis*, some sections of mature female worms were found free in the nasal cavity, but rarely; they had probably been displaced during histological processing. The oesophageal region, vagina, and posterior part of the female worms were in the epithelium (Figs 1C & D, 3A-C & H). This raises two questions: how are eggs expelled and how do the dwarf males enter the female vagina?

Eggs laid by *T. nasalis* were infiltrated between the female body wall and the epithelium of the mucosa (Fig. 3C). This explains why, during dissection, eggs and membranous debris were found adhering to the female's body. Small groups of eggs are also present in the lumen of the nasal cavities (Fig. 2E). They were probably freed by accidental rupture of the stretched and fragile epithelium. Egg expulsion thus differs only slightly from that of *Anatrichosoma* spp. from monkeys. Eggs of these species are grouped in tunnels formed by the female worms; the tubes containing eggs are sloughed off into the lumen in the course of the regenerative process of the multilayered epithelium (Orihel, 1970). In the species from monkeys, eggs were rarely found in the faeces; thus they must rarely be swallowed but rather expelled mainly through the nostrils (Orihel, 1970). The situation seems similar with *T. nasalis*, as very few eggs were found in the faeces of infected *A. niloticus*.

Concerning mating, two different behaviours are possible: luminal or tissular mating, as suggested by the studies performed with several Trichosomoidinae (Table I). In *T. crassicauda* mating seemed to occur in the lumen of the urinary tract, before the female penetrated the bladder epithelium (Thomas, 1924). If so, fertilized and relatively large adult females will penetrate in the epithelium, in contrast to previous studies on trichinelloids which demonstrated that a small first stage larva armed with a stylet typically invaded the mucosal epithelium (Wright, 1989; Anderson, 2000). In *A. haycocki* Spratt, 1982, a parasite of the paracloacal glands of Australian marsupials, mating also seems to be luminal, in the paracloacal glands (Spratt, 1982); the females of this species remained free in the lumen of the paracloacal glands or were encapsulated in host tissue in the lumen of the cloaca, whereas mature males were in the epithelium of the glands and in the surrounding connective tissue (Spratt, 1982).

The other behaviour is presented by *A. buccalis*, the unique trichosomoid species in which mating has been clearly observed: the male inserts the posterior half of the body into the female vagina (Little & Orihel, 1972). As the male lives in the lamina propria of the buccal mucosa and the female in the subadjacent multilayered epithelium (Pence & Little, 1972), the male has to migrate to the superficial layer (Little & Orihel, 1972). Males of *Anatrichosoma* spp. from monkeys probably have a similar behaviour, having a similar localization in the lamina propria of the mucosa (Allen, 1960; Long *et al.*, 1976; Takenaka *et al.*, 1989). A micrograph of *A. buccalis* males published by Pence & Little (1972) suggests that migrations might occur partly through the lymphatic vessels.

Although no male of *T. nasalis* was identified in the chorion, several features argue for the hypothesis of tissular mating in this species: *i)* no free males were recovered during dissection (Diagne *et al.*, 2000); *ii)* significant inflammatory infiltration was seen in the chorion of the nasal mucosa as with *Anatrichosoma* spp. from monkeys, the males of which reside in the chorion; *iii)* sections of females of *T. nasalis* in connective tissue suggested the existence of worm migration in deep organs, as exemplified by *T. crassicauda* (Yokogawa, 1921; Thomas, 1924). Indeed, *T. nasalis* first stage larvae probably hatch in the digestive tract, far from the nasal tissues. The migratory route of this species and the worm stage which will invade the nasal mucosa are presently undetermined.

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REFERENCES

Allen A.M. Occurrence of the nematode, *Anatrichosoma cutaneum*, in the nasal mucosae of *Macaca mulatta* monkeys. *American Journal of Veterinary Research*, 1960, *21*, 389-392.

Anderson R.C. Nematode parasites of vertebrates. Their development and transmission. 2nd Edition. CABI Publishing, Wallingford, UK, 2000, 650 p.

Antonakopoulos G.N., Turton J., Whitfield P. & Newman J. Host-parasite interface of the urinary bladder-inhabiting nematode *Trichosomoides crassicauda*: changes induced in the uroepithelium of infected rats. *International Journal for Parasitology*, 1991, *21*, 187-193.

Appleton J.A. New insights into the intestinal niche of *Trichinella spiralis*. *In*: Parasitic nematodes: molecular biology, biochemistry and immunology. Kennedy M.W. & Harnett W. (eds), CABI Publishing, Wallingford, UK, 2001, 103-120.

Beveridge I. & Barker I.K. *Nicollina antechini* sp. n. (Nematoda: Amidostomatidae) from the nasal cavity of the dasyurid marsupial, *Antechinus stuartii* Macleay, 1841, and associated pathology. *Journal of Parasitology*, 1975, *61*, 489-493.

Chitwood M.B. & Smith W.N. A redescription of *Anatrichosoma cynamolgi* Smith and Chitwood, 1954. *Proceedings of the Helminthological Society of Washington*, 1958, *25*, 112-117.

DIAGNE M., DIOUF M., LOCHOUARN L. & BAIN O. *Trichosomoides nasalis* Biocca & Aurizi, 1961 et *T. spratti* n. sp.(Nematoda: Trichinelloidea), parasites des fosses nasales de Muridés. *Parasite*, 2000, *7*, 215-220.

GARDINER C.H. Habitat and reproductive behavior of *Trichinella spiralis*. *Journal of Parasitology*,1976, *62*, 865-870.

KOZEK W.J. The molting pattern in *Trichinella spiralis*. I. A light microscope study. *Journal of Parasitology*, 1971a, *57*, 1015-1028.

KOZEK W.J. The molting pattern in *Trichinella spiralis*. II. An electron microscope study. *Journal of Parasitology*, 1971b, *57*, 1028-1038.

LEE T.D.G. & WRIGHT K.A. The morphology of the attachment and probable feeding site of the nematode, *Trichuris muris* (Schrank, 1788) Hall, 1916. *Canadian Journal of Zoology*, *56*, 1978, 1889-1905.

LITTLE M.D. & ORIHEL T.C. The mating behavior of *Anatrichosoma* (Nematoda : Trichuroidea). *Journal of Parasitology*, 1972, *58*, 1019-1020.

LONG G.G., LICHTENFELS J.R. & STOOKEY J.L. *Anatrichosoma cynamolgi* (Nematoda: Trichinellida) in rhesus monkeys, *Macaca mulatta*. *Journal of Parasitology*, 1976, *62*, 111-115.

LOWENSTEIN S. Epithelwucherungen und Papillombildungen der Rattenblase, verursacht durch die *Trichosoma* (*Tr. crassicauda*?). Vorläufige Mitteilung. *Beiträge zur klinischen Chirurgie*, 1910, *69*, 533-546.

MOREHOUSE N.F. Life cycle of *Capillaria caudinflata*, a nematode parasite of the common fowl. *Iowa State College Journal of Science*, 1944, *18*, 217-253.

ORIHEL T. C. Anatrichosomiasis in African monkeys. *Journal of Parasitol*ogy, 1970, *56*, 982-985.

PENCE D.B. & LITTLE M.D. *Anatrichosoma buccalis* sp. n. (Nematoda: Trichosomoididae) from the buccal mucosa of the common opossum, *Didelphis marsupialis*. *Journal of Parasitol*ogy, 1972, *58*, 767-773.

SERAKIDES R., RIBEIRO A.F.C., SILVA C. M., SANTOS R.L., NUNES V.A. & NASCIMENTO E.F. Proliferative and inflammatory changes in the urinary bladder of female rats naturally infected with *Trichosomoides crassicauda*: reports of 48 cases. *Arquivo Brasileiro de Medicina Veterinària e Zootecnia*, 2001, *53*, 1-5.

SPRATT D.M. *Anatrichosoma haycocki* sp. n. (Nematoda: Trichuridae) from the paracloacal glands of *Antechinus* spp., with notes on *Skrjabinocapillaria* Skarbilovitsch. *Annales de Parasitologie Humaine et Comparée*, 1982, *57*, 63-71.

SWIFT H.F., BOOTS R.H. & MILLER C.P. A cutaneous nematode infection in monkeys. *Journal of Experimental Medicine*, 1922, *35*, 599-620.

THAPAR G.S. & SINGH K.R.S. Studies on the life-history of *Trichuris ovis* (Abildgaard, 1795) (Fam. Trichuridae: Nematoda). *Proceedings of the Indian Academy of Sciences*, 1954, *11*, 69-98.

THOMAS L.J. Studies on the life history of *Trichosomoides crassicauda* (Bellingham). *Journal of Parasitology*, 1924, *10*, 105-135.

TAKENAKA T., UEKI H., HASHIMOTO Y., HASHIMOTO K. & MATSYMOTO S. A survey for prevalence of *Anatrichosoma* sp. in nasal cavities of *Cynomolgus* monkeys. *Experimental Animals* (Jikken Dobotsu), 1989, *38*, 93-96.

WEHR E.E. Studies on the development of the pigeon capillarid, *Capillaria columbae*. *Technical Bulletin*, U.S.D.A., 1939, *679*, 1-20.

WRIGHT K.A. Observation on the life cycle of *Capillaria hepatica* (Bancroft, 1893) with a description of the adult. *Canadian Journal of Zoology*, 1961, *38*, 167-182.

WRIGHT K.A. Parasites in peril - the trichuroid nematodes. *In*: Current Concepts in Parasitology. Ko R. (ed.), Hong Kong University Press, Hong Kong, 1989, 65-80.

YOKOGAWA S. On the migratory course of *Trichosomoides crassicauda* (Bellingham) in the body of the final host. *Journal of Parasitology*, 1921, *7*, 80-84.

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