SECTION 3

PARASITES

OF

REPTILES

Introduction

The parasites of reptiles are poorly known in South Africa. Dr. Stephan Hering-Hagenbeck came to this country to initially do the helminths of nyalas, but I convinced him to rather do the helminths of reptiles. He sought, and got, permission to collect from a number of geographical regions, and recorded a whole host of new species. I was one of his co-promoters, and some of the funding was borne by my laboratory. What follows is a selection of the papers that were published from his PhD thesis on snakes and lizards.

As stated earlier, Dr Junker arrived in South Africa to do the pentastomid parasites of fish and crocodiles. Again, a selection of papers produced as result of her research on pentastomids and the results of some routine identifications or crocodile helminths are presented here.

The section is arranged in two chapters, the helminths and pentastomes, and within each chapter the papers are listed firstly by the species descriptions in chronological order and then by the helminth communities, also chronologically.

HELMINTH PARASITESS OF REPTILES (P 519)

HERING-HAGENBECK, S.F.B.N & BOOMKER, J. 1998. *Spauligodon timbavatiensis* n. sp. (Nematoda: Pharyngodonidae) from *Pachydactylus turneri* (Sauria: Gekkonidae) in the Northern Province, South Africa. *Onderstepoort Journal of Veterinary Research*, 65, 153 – 158.

HERING-HAGENBECK, S., BOOMKER, J., PETIT, G., KILLICK-KENDRICK, M. & BAIN, O. 2000. Description of *Madathamugadia hiepei* n. sp. (Nematoda: Splendidofilariinae), a parasite of a South African gecko, and its development in laboratory bred *Phlebotomus dubosqi* (Diptera: Psychodidae). *Systematic Parasitology*, 47, 207-213.

HERING-HAGENBECK, S.F.B.N., PETTER, A.J. & BOOMKER, J. 2002. Redesription of some *Spauligodon* spp. and of *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968 (Pharyngodonidae: Oxyuroidea) from insectivorous South African lizards. *Onderstepoort Journal of Veterinary Research*, 69, 7-29.

HERING-HAGENBECK, S.F.B.N., PETTER, A.J. & BOOMKER, J. 2002. Redescription of some *Thelandros* and *Tachygonetria* spp. (Pharyngodonidae: Oxyuroidea) from the omnivorous plated lizard, *Gerrhosaurus validus validus* A. Smith, 1849 in South Africa. *Onderstepoort Journal of Veterinary Research*, 69, 31-51.

JUNKER, K., WALLACE, K., LESLIE, A.J. & BOOMKER, J. 2006. Gastric nematodes of Nile crocodiles, *Crocodilus niloticus* Laurenti, 1768, from the Okavango River, Botswana. *Onderstepoort Journal of Veterinary Research*, 73, 111-114.

JUNKER, K., BAIN, O. & BOOMKER, J. 2006. *Eustrongylides* sp. (Nematoda: Dioctophymatoidea) from the stomach of a Nile crocodile, *Crocodylus niloticus* Laurenti, 1768, in Botswana. *Onderstepoort Journal of Veterinary Research*, 73, 315-317.

HERING-HAGENBECK, S.F.B.N. & BOOMKER, J., 2000. A check list of the nematode parasites of South African Serpentes (snakes) and Sauria (lizards). *Onderstepoort Journal of Veterinary Research*, 67, 1 - 13.

PENTASTOMID PARASITESS OF REPTILES (P 599)

JUNKER, KERSTIN, BOOMKER, J., BOLTON, LORNA A. 1999.Pentastomid infections in Nile crocodiles (*Crocodylus niloticus*) in the Kruger National Park, South Africa, with a description of the males of *Alofia simpsoni*. *Onderstepoort Journal of Veterinary Research*, 66, 65-71.

JUNKER, K., BOOMKER, J., SWANEPOEL, D. & TARASCHEWSKI, H. 2000. *Leiperia cincinnalis* Sambon, 1922 (Pentastomida) from Nile crocodiles *Crocodylus niloticus* in the Kruger National Park, South Africa, with a description of the male. *Systematic Parasitology*, 47, 29 – 41.

JUNKER, K. & BOOMKER, J. 2002. Description of *Pelonia africana* n.g., n. sp. (Pentastomida: Sebekidae) from the lungs of *Pelomedusa subrufa* and *Pelusios siniatus* (Chelonia) in South Africa. *Onderstepoort Journal of Veterinary Research*, 69, 53-59.

JUNKER, K., RILEY, J & BOOMKER, J. 2003. Redescription of of *Diesingia megastoma* (Diesing, 1836) Sambon, 1922, a pentastomid parasite from the South American terrapin *Hydromedusa tectifera* Cope. *Systematic Parasitology*, 56, 211-218.

JUNKER, K. & BOOMKER, J. 2006. A check-list of the pentastomid parasites of crocodilians and freshwater chelonians. *Onderstepoort Journal of Veterinary Research*, 73, 27-36.

CHAPTER 1

Helminth parasites

of

reptiles

Onderstepoort Journal of Veterinary Research, 65:153–158 (1998)

Spauligodon timbavatiensis n. sp. (Nematoda: Pharyngodonidae) from *Pachydactylus turneri* (Sauria: Gekkonidae) in the Northern Province, South Africa

S.F.B.N. HERING-HAGENBECK[1] and J. BOOMKER[2]

ABSTRACT

HERING-HAGENBECK, S.F.B.N. & BOOMKER, J. 1998. *Spauligodon timbavatiensis* n. sp. (Nematoda: Pharyngodonidae) from *Pachydactylus turneri* (Sauria: Gekkonidae) in the Northern Province, South Africa. *Onderstepoort Journal of Veterinary Research*, 65:153–158

Spauligodon timbavatiensis n. sp. (Nematoda: Pharyngodonidae) from the large intestine of *Pachydactylus turneri* (Sauria: Gekkonidae) in the Northern Province (RSA) is described and illustrated. It is the fifth species in the Ethiopian region, the others being *Spauligodon smithi* from *Pachydactylus bibronii* and *Spauligodon petersi* from *Mabuya sulcata*, both in the Northern Cape Province, South Africa, *Spauligodon morgani* from *Mabuya striata* in Malawi, and *Spauligodon dimorpha* from *Chamaeleo pardalis* in Madagascar.

The males of the new species differ from *S. smithi* in that the adcloacal papillae are single (bifid in *S. smithi*), from *S. petersi* in the presence of a spicule and having narrow lateral alae (wide and triangular in *S. petersi*) and from *S. dimorpha* and *S. morgani* in having a spicule. Furthermore, *S. timbavatiensis* differs from *S. morgani* in lacking spines on the tail. The females of the new species have a long tail and truncated egg ends as opposed to the short, spiky tail and pointed eggs of *S. morgani*; a spiny tail and truncated eggs as opposed to the smooth tail and pointed eggs of S. *petersi* and a longer oesophagus than *S. smithi*. Furthermore, the females of *S. dimorpha* and *S. morgani* are much larger than those of *S. timbavatiensis*. In addition, the excretory pore opens behind the posterior end of the oesophageal bulb in the new species, while in *S. smithi* and *S. dimorpha* it opens at the level of the end of the oesophageal bulb.

Keywords: Gekkonidae, nematode, *Pachydactylus turneri*, Pharyngodonidae, reptiles, South Africa, *Spauligodon timbavatiensis* n. sp.

INTRODUCTION

As part of a study on the parasites of reptiles, several species of Sauria were collected from the Klaserie Private Game Reserve, Northern Province, South Africa. Among these were two specimens of *Pachydactylus turneri*, a common large gecko in southern Africa. They occur on rocky outcrops, under loose tree bark and sometimes on houses. The geckos are gregarious and are often found in colonies. Their prey consists of a variety of insects including ants, termites, beetles and grasshoppers, and even smaller lizards are consumed on occasion (Branch 1998). The *Pachydactylus bibronii-laevigatus* complex was recently revised (Benyr 1995), but Branch (1998) does not accept this revision.

The genus *Spauligodon* was created when the genus *Pharyngodon* Diesing, 1861 was divided into three new genera: *Pharyngodon, Parathelandros* Baylis, 1930 and *Spauligodon* Skrjabin, Schikhobalova & Lagodovskaja, 1960 (Skrjabin, Schikhobalova & Lagodovskaja 1960). Thirty-four *Spauligodon* species have as yet been described, four of which occur in the Ethiopian region (Bursey, McAllister & Freed 1997).

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In this paper the fifth species, recovered from the large intestine of the geckos and for which the name *Spauligodon timbavatiensis* n. sp. is proposed is described and illustrated.

MATERIAL AND METHODS

Two geckos were collected by hand in the Klaserie Private Game Reserve and taken back alive to the laboratory. They were euthanazed, weighed and measured, and the internal organs removed. The trachea, lungs, liver, oesophagus, stomach, small intestines, large intestines and rectum were placed in phosphate buffered saline (PBS) in separate petri dishes, and examined for helminths under a stereoscopic microscope. In order to obtain clean specimens, nematodes were removed from the ingesta, placed in another petri dish in PBS for 20–30 min, whereafter they were fixed in boiling 70% ethanol. For detailed light microscopic studies they were transferred to a 50% lactophenol-water solution and examined while clearing. The material was studied under a Nikon compound microscope and drawings made with a drawing tube. Measurements were made by measuring the drawings. Measurements are those of the holotype and allotype and, where available, followed by those of the paratypes (in parentheses). All measurements are given in millimeters (mm).

Specimens for scanning electron microscopy were dehydrated through graded ethyl alcohol and critical point dried. They were sputter coated with gold and examined with a Leica Stereoscan 420 scanning electron microscope at an accelerating voltage of 5 kV.

The geckos were deposited in the herpetological collection of the Transvaal Museum (TM. 81535 and TM. 81536).

RESULTS

Characterization of the genus *Spauligodon* Skrjabin, Schikhobalova & Lagodovskaja, 1960

Pharyngodonidae with a triangular mouth opening, each lip partially or completely divided into two. Excretory pore behind the oesophageal bulb, in females always near the vulva. Oesophageal bulb with a well-sclerotized valvular apparatus. Lateral alae are present. The cloacal papillae of the males are clearly separated into precloacal, adcloacal and postcloacal pairs. Papillae of the last named pair are well separated from each other and usually only a short distance from the adcloacal pair and never rosette-shaped. The protruding genital cone may be supported by sclerotized structures, but the pre- and adcloacal pairs of papillae are never situated on the cone. Caudal alae are always present, but never support the last pair of papillae. Spicules are often absent. The usually long and tapering tail may be spinose or aspinose (amended from Skrjabin *et al.* 1960 and Petter & Quentin 1976). Parasites of carnivorous reptiles.

DESCRIPTION OF THE SPECIES

Spauligodon timbavatiensis n. sp. (Fig. 1 and 2)

Small nematodes with a cylindrical body, tapering at both ends. In both sexes lateral alae are present and the nerve ring surrounds the oesophagus in the anterior half, more or less at the commencement of the lateral alae. The conspicuous excretory pore always lies posterior to the oesophageal bulb and is a transverse slit surrounded by a chitinous rim. The tail is long and flexible.

MALES

Small nematodes, 2,24 (1,74–2,05) long and 0,19 (0,12–0,14) wide at mid-body. Three well-developed lips surround a triangular mouth opening. Each lip is incompletely divided in two lobes with a shallow notch in each lobe. Cephalic papillae were not seen. Behind the anterior margin of the lips, on their inner side, two tooth-like structures are visible.

Narrow lateral alae start at 0,09 (0,12–0,18) and 0,14 (0,12–0,15), respectively, from the anterior end, and are 1,54 (1,49–1,83) and 1,49 (1,47–1,82) long.

The oesophagus consists of a fairly short, clavate corpus, 0,26 (0,26–0,35) long, before it joins the slightly oval bulbus that is 0,09 (0,07–0,08) long and 0,07 (0,07–0,08) wide. The nerve ring and excretory pore are situated 0,15 (0,12–0,15) and 0,65 (0,56–0,65), respectively, from the anterior end.

The cloacal papillae comprise a pair of pre-cloacal papillae, a pair of adcloacal papillae and a pair of post cloacal papillae. Caudal alae have a finely sculptured inner surface. A characteristic genital cone surrounded by an ornate, folded membranous lip is present. Only one very weakly sclerotized spicule measuring 0,08 is visible. The tail is 0,25 (0,17–0,24) long and aspinose.

FEMALES

Females are larger than males, 3,49 (2,13–2,41) long and 0,22 (0,21–0,27) wide at mid-body. As in the males, there are three well-developed lips surrounding a triangular mouth opening. Each lip is divided into two lobes and tooth-like structures are borne on the inside of each lip. Cephalic papillae were not seen.

The lateral alae start at 0,14 (0,09–0,12) from the anterior end and are 2,54 (2,15–2,46) long and 0,02 wide.

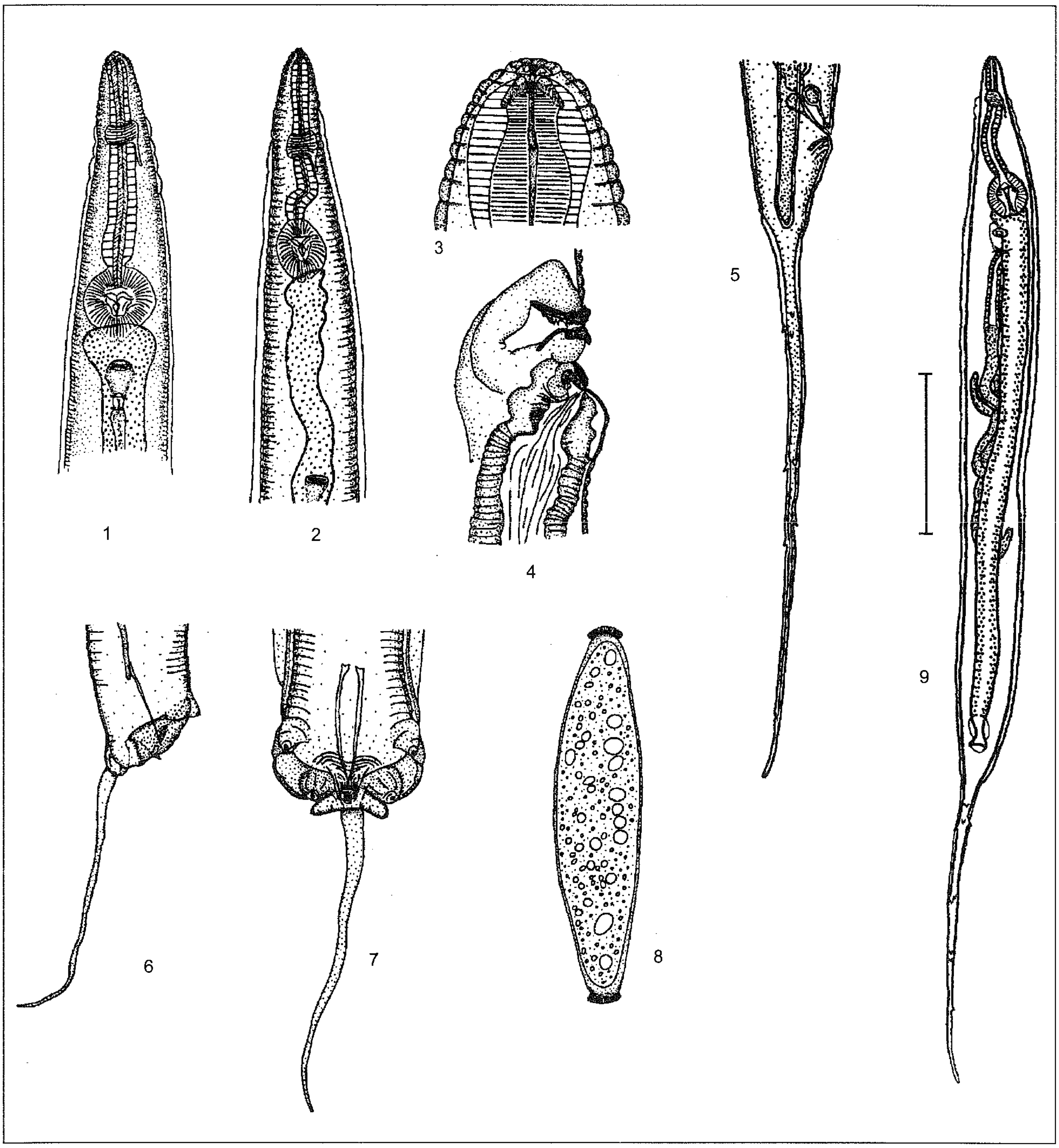

FIG. 1 *Spauligodon timbavatiensis* n. sp.

1. Anterior part, ventral view, paratype male (bar = 0,1 mm)
2. Anterior part, ventral view, paratype female (bar = 0,1 mm)
3. Detailed anterior part, ventral view, paratype female (bar = 0,05 mm)
4. Vulva and excretory pore, lateral view, paratype female (bar = 0,1 mm)
5. Posterior end, lateral view, paratype female (bar = 0,05 mm)
6. Posterior end, lateral view, paratype male (bar = 0,1 mm)
7. Posterior end, ventral view, paratype male (bar = 0,1 mm)
8. Egg (bar = 0,1 mm)
9. Entire, lateral view, paratype female (bar = 0,5 mm)

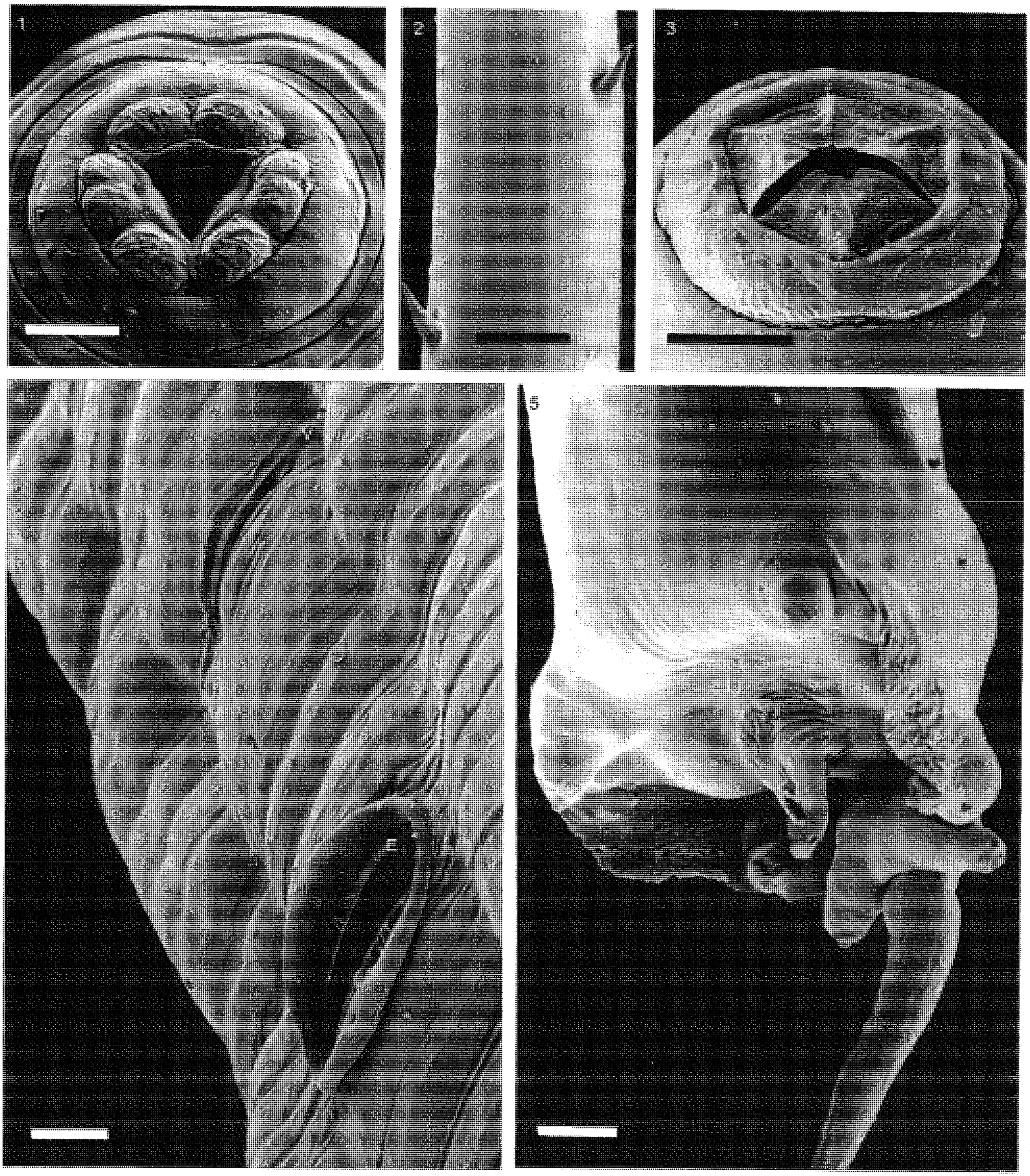

FIG. 2 *Spauligodon timbavatiensis* sp. n.

1. Anterior part, paratype female
   (bar = 0,05 mm)
2. Spines on tail of paratype female
   (bar = 0,05 mm)
3. Anterior part, paratype male
   (bar = 0,05 mm)
4. Midbody paratype female, V = vulva; E = excretory pore
   (bar = 0,05 mm)
5. Posterior part, paratype male
   (bar = 0,09 mm)

The body of the oesophagus is 0,41 (0,37–0,40) long, and the bulb 0,14 (0,11–0,14) long and 0,14 (0,14–0,15) wide. The nerve ring and excretory pore are situated 0,16 (0,13–0,17) and 0,62 (0,57–0,63) from the anterior end, respectively.

The vulva lies slightly behind the excretory pore, 0,68 (0,56–0,66) from the anterior end. The muscular ovejector extends posteriorly into a thin-walled common uterus, 0,33 long, into which join the anterior and posterior uteri. Thin-shelled eggs in the uterus measure 0,156 (0,133–0,162) x 0,033 (0,032–0,034), and are elongated and fusiform, with caps on each truncated end. They are unsegmented when laid. The long, flexible, filiform tail, 0,96 (0,83–1,11) long, always carries between seven and nine cuticular spines.

TYPE HOST

Pachydactylus turneri (Gekkonidae).

TYPE LOCALITY

Timbavati/Klaserie/Umbabat Private Nature Reserves (25°36´51,8´´S; 28°01´30,5´´E), Northern Province, Republic of South Africa.

TYPE MATERIAL

Holotype male, allotype female, ten paratype males and ten paratype females. The paratypes included immature males and females without eggs. The type specimens are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 579HF.

HABITAT

Mucosa of large intestine.

ETYMOLOGY

The species is named after the locality of the host.

DISCUSSION

The general morphology of the new species allows its inclusion into the family Pharyngodonidae. Only in the genera *Pharyngodon* (syn. *Neopharyngodon* Chakravarty & Bhaduri, 1948), *Skrjabinodon* Inglis, 1968 and *Spauligodon* does the vulva open just behind the post bulbar excretory pore in the anterior part of the body. In contrast to the males of *Pharyngodon*, which have well-developed caudal alae enveloping all genital papillae, *Skrjabinodon* males lack the caudal alae, while the males of *Spauligodon* have caudal alae that do not enclose the posterior pair of papillae. Based on the position of the vulva and the configuration of the caudal alae of the male, the new species conforms to the description of the genus *Spauligodon*.

There currently are 34 species of *Spauligodon* that are separated on the presence or absence of spines on the tail and the shape of the eggs (Bursey & Goldberg 1995). However, Chabaud & Brygoo (1962) suggested that the most important factor in speciation of reptilian oxyurids would be the geographical distribution. Only four *Spauligodon*-species have presently been described for the Ethiopian region. Three of these, *S. dimorpha*, *S. morgani* and *S. petersi* lack spicules. The females of *S. dimorpha* and *S. morgani* are much larger than those of *S. timbavatiensis*, their tails are short and the excretory pore of *S. dimorpha* is situated on the same level as the oesophageal bulb. *S. dimorpha* was described from *Chamaeleo pardalis* in Madagascar (Chabaud & Brygoo 1962). Furthermore, the males of *S. morgani* have a spinose tail and the species was described from *Mabuya striata* in Malawi (Fritzsimmons 1961).

The female of *S. petersi* lacks spines on the tail and the male has wide lateral alae. In addition, the eggs are pointed with smaller terminal plugs on each end and are flattened on one side. *S. petersi* was described from *Mabuya sulcata sulcata* in South Africa (Bursey *et al.* 1997).

The remaining species, *S. smithi*, is very similar to *S. timbavatiensis* as regards the host and locality. The most conspicuous difference is that the adcloacal pair of papillae is bifid in *S. smithi* and single in *S. timbavatiensis*. Furthermore, the excretory pore and vulva of female *S. smithi* are situated more anterior than in *S. timbavatiensis*, although the body lengths are nearly the same. Both sexes of the last named species also have slightly oval oesophageal bulbs as opposed to the round bulb in both sexes of *S. smithi*.

We believe that the differences between the new and already described species are sufficient to warrant the creation of a new species, for which the name *S. timbavatiensis* n. sp. is proposed.

ACKNOWLEDGEMENTS

We wish to express our appreciation to the following persons and institutions: Dr Salomon Joubert, Mr Brian Harris, Mr Collin Rowles and the private landowners for permission to do the field collection in the Timbavati/Klaserie/Umbabat Private Game Reserves; Mr Wulf Haacke and Mr Richard Newbery for much help as regards the reptiles; the Department of Environmental Affairs, Northern Province, for the collecting permits; Miss Chantelle Baker and Miss Nishi Prabdial, Medical University of Southern Africa, for help in preparing and scanning of the specimens.

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Description of *Madathamugadia hiepei* n. sp. (Nematoda: Splendidofilariinae), a parasite of a South African gecko, and its development in laboratory bred *Phlebotomus dubosqi* (Diptera: Psychodidae)

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Abstract

Madathamugadia hiepei n. sp., Splendidofilariinae, a parasite of a South African gecko *Pachydactylus turneri* is described together with its development obtained experimentally in *Phlebotomus duboscqi* (Diptera: Psychodidae: Phlebotominae). This new species differs from the two small, more highly evolved groups with a short tail and atrophied postcloacal papillae, the first group consisting of two Madagascan species, *M. zonosauri* and *M. hopluri*, parasites of the Gerrhosauridae and Iguanidae, and the second containing three species from the Ethiopian Region, *M. huambensis*, *M. versterae* and *M. bissani*, parasites of the Scincidae. It also differs from *M. ineichi*, the most primitive species of the genus (cuticularised buccal capsule, no atrophy of head papillae and largest number of precloacal papillae), a parasite of the Cordylidae in South Africa. *M. hiepei* is close to the two species parasitic in the Gekkonidae of the Mediterranean subregion, *M. ivaschkini* and *M. wanjii*, all three of which have a post-oesophageal vulva. However, the new species can be distinguished from the Mediterranean parasites by (a) the shorter oesophagus, (b) the number and position of the cloacal papillae and (c) the microfilaria. The three filariae of this group and *M. ineichi*, the only ones of which aspects of the life-cycles are known, experimentally develop in phlebotomine sand flies.

Introduction

Three genera of filarial worms of the subfamily Splendidofilariinae are parasites of saurians: *Thamugadia* Seurat, 1917 from the Mediterranean subregion represented by four species (Seurat, 1917; Sulahian & Schacher, 1968; Annaev & Sonin, 1973; Bain et al., 1993); *Pseudothamugadia* Lopez-Neyra, 1956 from Australia which is monospecific (Johnston, 1912); and *Madathamugadia* Chabaud, Anderson & Brygoo, 1959 which is comprised of two Madagascan species (Chabaud et al., 1959), two from the Mediterranean subregion (Bain et al., 1992) and four from the Ethiopian Region (Bain et al., 1993).

The filariid described in the present paper belongs to the last of these genera, *Madathamugadia*, which is characterized by the presence of precloacal papillae of the male and dissimilar left and right spicules (Bain et al., 1992). It was collected from a South African gecko, *Pachydactylus turneri* (Gray). *Madathamugadia* was known previously only from the Scincidae and Cordylidae of the Ethiopian Region and the Gekkonidae of the Mediterranean subregion.

The larval development of three *Madathamugadia* species have been seen in experimentally infected sand flies (Reznik, 1982; Bain et al., 1992, 1993). For this reason, sand flies were used in the present study.

Materials and methods

Pachydactylus turneri, a common, large thick-toed gecko, is widely distributed in the northern parts of southern Africa where it occurs on rocky outcrops, often living in colonies (Branch, 1998). The systematics of the *P. bibronii-laevigatus-turneri* complex is currently not clear (Benyr, 1995; Branch, 1998; Haacke, 1998, pers. com.).

As part of a study of nematode parasites of reptiles in various places in South Africa (Hering-Hagenbeck & Boomker, 1998), 60 specimens of this gecko were caught in two different areas of the former Transvaal, Republic of South Africa. Microfilaraemia was determined in Giemsa-stained blood films. In the Hoedspruit Nature Reserve/Timbavati-Klaserie Private Game Reserves, Northern Province (24°04′23″ S; 31°03′18″ E), none of 22 geckos caught was infected. In contrast, in the campus of the Medical University of Southern Africa, Gauteng Province (25°36′51″ S; 28°01′30″ E), 25 of 38 geckos were infected with the new parasite (65.7%); however, microfilariae were seen only in the blood of adults and not in the blood of juveniles or subadults.

Six geckos with microfilariae in the blood were imported into France under a permit issued by Ministry of the Environment. They were kept in captivity in Paris to recover adult worms and study the life cycle. All six had concomitant infections with blood Protozoa. The filarial worms were situated in the dorsal parietal peritoneum, often under the intestine or rectum, sometimes more anteriorly under the lungs, and were inside thin-walled, transparent pockets which are probably dilated lymphatic vessels. Adults were non-motile and could be detected only by examination with a dissecting microscope. They became active when liberated into the dissecting medium, RPMI 1640 supplemented with 20% calf serum.

Wild sand flies were collected in the habitat of the geckos and dissected. Larval development was studied experimentally in *Phlebotomus duboscqi* Neveu-Lemaire from a colony originating from Keur Moussa, Senegal, and maintained by the methods described by Killick-Kendrick & Killick-Kendrick (1987). A single breeding box containing larvae and nymphs was used. The majority of adult flies emerged within 3 days; they were daily collected and placed in 3 cages. A parasitised gecko (217ES) restrained in a wire mesh was placed successively in these cages of sand flies. Fed female flies were collected each day, maintained at 25 °C and dissected 7 days later. A total of 70 sand flies were fed, although not all were used for the filarial cycle, because some were reserved to study the development of blood protozoa. Infective larvae obtained experimentally were inoculated in a single dose to a gecko which was necropsied 8 days later.

Adult worms were fixed in hot 70% ethanol, cleared in lactophenol and all examined. Blood microfilariae from the geckos were studied with vital Meldolan Blue staining and in Giemsa-stained thick blood films. Developing larvae were examined alive in the dissecting medium. All filarial stages were studied under a compound microscope and illustrated using a camera lucida. Measurements were made after drawings and are given in micrometres, unless otherwise specified.

Geographical regions are named after the Physical Geographic Atlas of the World Anonymous, 1964).

***Madathamugadia hiepei* n. sp.** (Figures 1–3)

Type-host: Pachydactylus turneri (Gray) (Gekkonidae).
Site: Peritoneal wall.
Type-locality: Campus of the Medical University of Southern Africa, Gauteng Province, Republic of South Africa.
Type-material (collection number followed by the number of the host): Holotype female 213ES (477); allotype male 213ES (477) and paratypes 213ES: three males, four females and a posterior region of each sex. Housed in the collection of the Muséum National d'Histoire Naturelle, Paris.
Other material: 215ES (475), one female; 217ES, two females (with developing eggs but no microfilariae) and two males, 218ES (476), one young female. 217ES is deposited in the collection of the Muséum National d'Histoire Naturelle, Paris; 213 ES, 215ES and 218ES are deposited in the collection of the Transvaal Museum, Pretoria.

Description

Mouth, buccal cavity and oesophageal lumen laterally flattened. Head papillae partly atrophied: 4 external labial papillae present, but only 2 of the 4 cephalic papillae. Oesophagus short and clearly divided, often with 3 conspicuous glandular pores (close to nerve-ring, at mid-length and posterior third of glandular oesophagus). Anterior intestinal wall with granules regularly disposed.

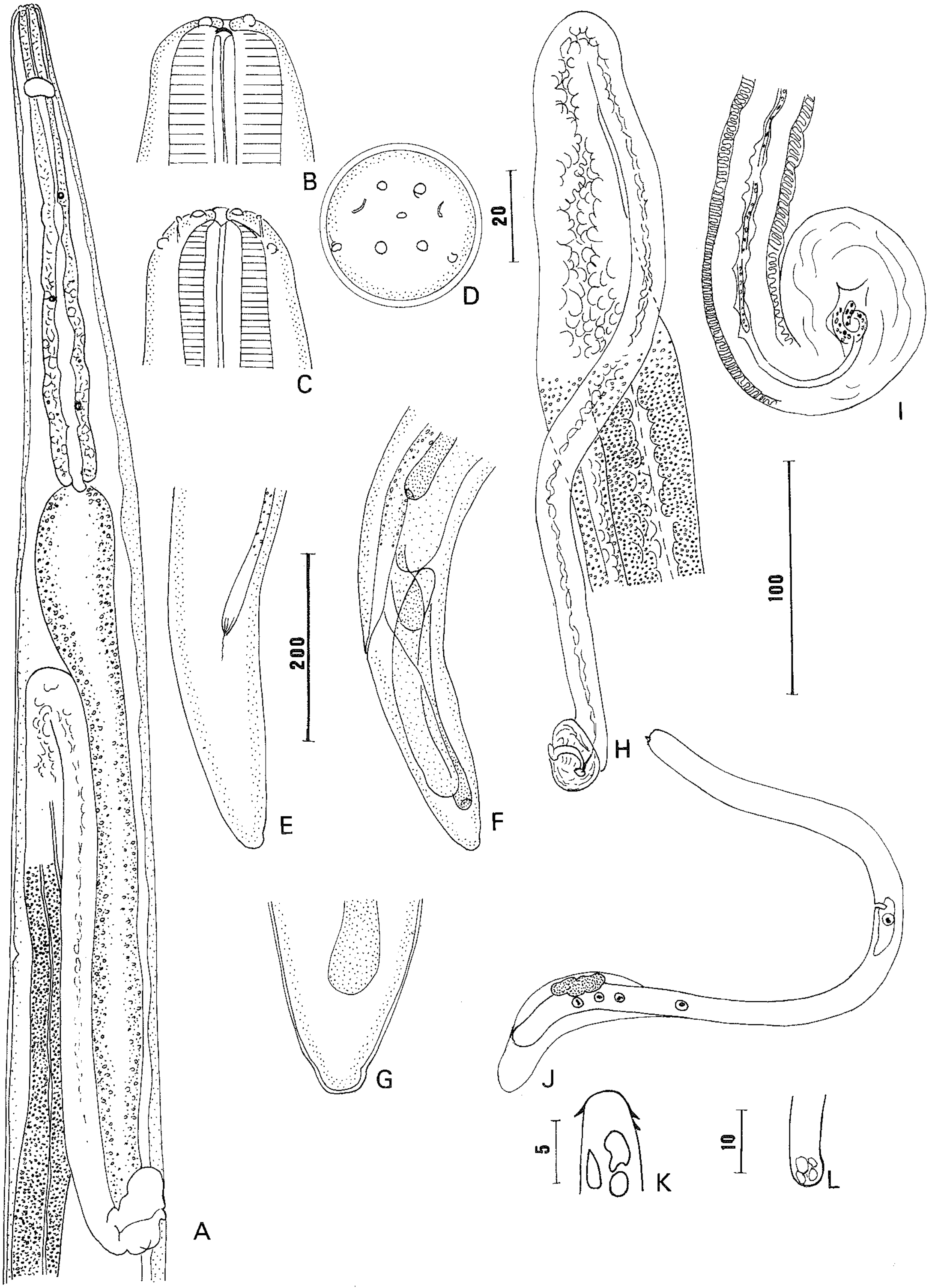

Figure 1. Madathamugadia hiepei n. sp., female: A. Anterior region, lateral view; B & C. Head, lateral and median view; D. Apical view of the head of a paratype; E & F. Tail, median and lateral view; G. Caudal extremity, dorso-median view; H. Vagina and ovijector of a paratype; I. Detail of vagina; J. Microfilaria, in vital coloration; K. & L. Detail of head and caudal extremity of a microfilaria. *Scale-bars:* A,E,F,H, 200 μm; B,C,D, 20 μm; G,I, 100 μm; J,L, 10 μm; K, 5 μm.

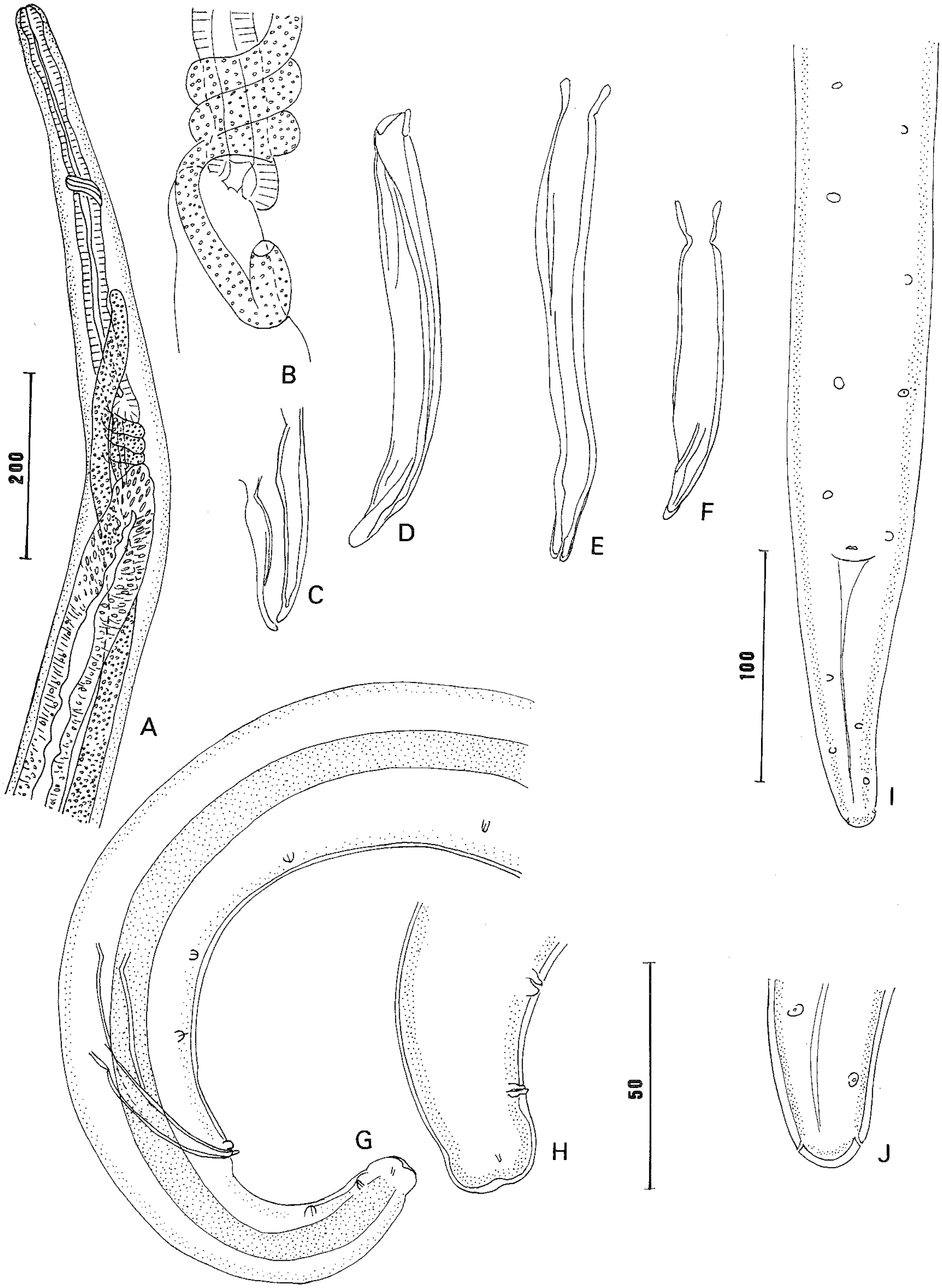

Figure 2. Madathamugadia hiepei n. sp., male. A. Anterior region of a paratype, lateral view; B. Oesophageal intestinal junction and testis, lateral view; C. Spicules, ventral view; D-E. Left spicule, lateral and ventral view; F. Right spicule, lateral view; G. Male allotype, posterior region, lateral view; H. Caudal extremity, lateral view; I. Paratype, ventral view; J. Caudal extremity, ventral view. *Scale-bars:* A, 200 μm; B,C,G,I, 100 μm; D,E,F,H,J, 50 μm.

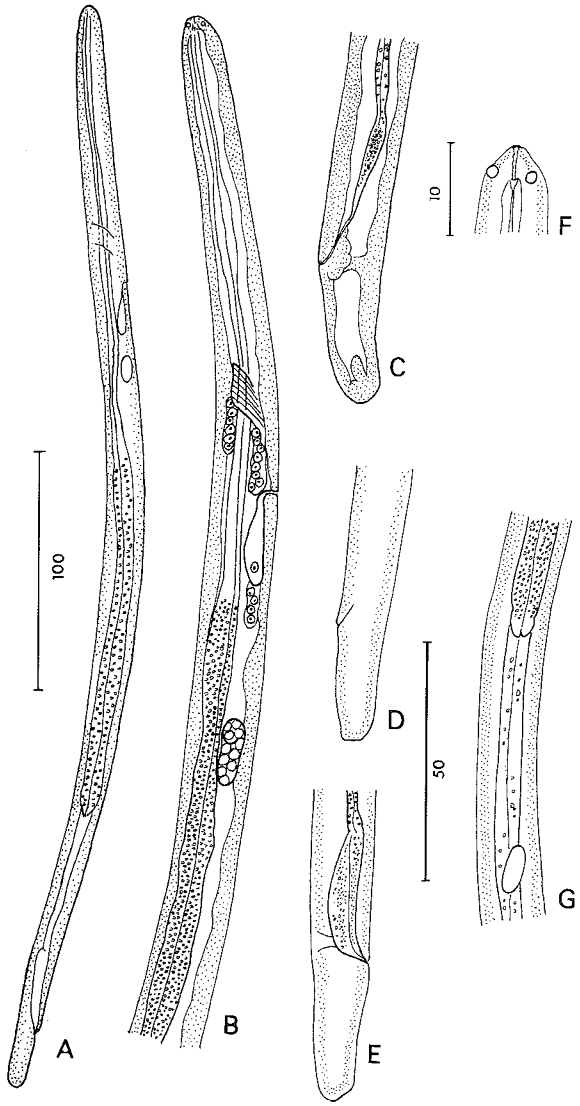

Figure 3. Madathamugadia hiepei n. sp., infective larva. A. Female, general aspect, lateral view; B. Anterior region of another larval female, with genital primodium at level of glandular oesophagus, lateral view; C. Tail, lateral view; D-E. Two other tails, lateral view; F. Head, median view; G. Male, genital primodium posterior to oesophageal intestinal junction, lateral view. *Scale-bars:* A, 100 μm; F, 10 μm; others, 50 μm.

Female (measurements of holotype, one paratype and, in parentheses, 2 females 217 ES). Body length 15.52, 14.66 (12.8, 12.15) mm, width 230, 175 (190, 120); nerve-ring 245, 195 (220, 180) from apex; oesophagus 445, 490 (475, 500) long; vulva in mature females post-oesophageal, 990, 1125 (940, 1070) from apex; ovijector wider in posterior third, just before dividing in 2 uteri, 1300, 970 long; ovaries coiled in posterior part of body; tail 290, 330 (200, 225) long.

Young female (218 ES): body length 8.4 mm, widt 145; oesophagus 550 long with muscular portion 25 long; vulva at level of oesophagus, near junction wit intestine, 550 from apex; tail 345 long (Figure 1).

Microfilaria (mean measurements of 7 specimen and range in parentheses). 147.8 (140–155) long an 4.5 (4–5.5) wide; corpuscle 7 to 10 long. Sheat inflated posteriorly; at this level, refringent, ovoi corpuscle; head more or less as wide as body; lef cephalic hook and 2 right spines; caudal extremit thick even sometimes inflated, rounded, with 2–3 terminal nuclei (Figure 1).

Male (measurements of the allotype, one paratype and, in parentheses, 2 males 217 ES). Body 10.62, 9.97 (11.1, 9.9) mm long, width 118, 108 (135, 135); nerve-ring 223, 195 (210, 240) from apex; oesophagus 570, 515 (450, 475) long. 6 pairs of caudal papillae, 4 precloacal and 2 postcloacal. Tail 117, 100 (98, 110) long. Left and right spicules different in shape and size, respectively 114, 97 (93, 92) and 80, 82 (70, 68) (Figure 2).

Larval development

Approximately 100 specimens of a *Sergentomyia* sp. were collected in the habitat of the geckos; they were not found infected.

In *P. duboscqi*, the infective larvae (Figure 3) developed within 7 days. A total of 15 infective larvae were recovered from a batch of 20 sand flies fed the same day on the infected gecko. Three were used for the morphological study. Head attenuated, with buccal capsule cuticularised at its basement; only cephalic papillae visible; oesophagus divided, glandular part irregularly granulated; ratio length of oesophagus/bodylength 55–85%; tail without caudal lappets, straight or slightly bent in posterior third, cylindrical or slightly tapered, or with subterminal constriction; female genital primordium at level of muscular oesophagus; male genital primordium at level of intestine.

Measurements (2 female and one male infective larvae). Body length 490, 410, 480; width 16, 17, 15; buccal cavity 4, 4, 3 long; oesophagus 270, 350, 300 in length with muscular portion 120, 110, 130. Nerve ring 80, 100, 80, excretory pore 108, 140, 132, and female genital primordium 130, 170, all respectively from anterior end. Tail length 32, 30, 27.

Younger stages were collected in the thoracic muscles of the intermediate host. Larva at first moult 90 long and 22 wide; larva at second moult 335 long and 19 wide; length of oesophagus 180.

Among the 10 infective larvae inoculated to the gecko, 4 were recovered 8 days later. Three of the larvae were in the subcutaneous tissue and not very motile; one very motile larva was found in the dissecting medium (unfortunately these larvae were lost).

Discussion

The genus *Madathamugadia* is comprised of eight species divided into four groups (Bain et al., 1993), all different from the material studied in the present work:

– The two Madagascan species, *M. zonosauri* Chabaud, Anderson & Brygoo, 1959 and *M. hopluri* Chabaud, Anderson & Brygoo, 1959, are respectively parasites of the Gerrhosauridae and Iguanidae. Their males have a short conical tail (with the length equalling the width at the level of the anus), without postcloacal papillae or with a single pair near the cloaca; the pairs of pre-cloacal papillae are reduced in number (two and three pairs); the vulva is at the level of the oesophagus, not far from the junction with the intestine; and the microfilariae are notably small (a third of the length of those of our parasite).

– The three species parasitic in the Scincidae of the Ethiopian Region, *M. huambensis* (Petit, Bain, Gomes & Touratier, 1983), *M. versterae* Bain, Wanji, Petit, Paperna & Finkelman, 1993 and *M. bissani* Bain, Wanji, Petit, Paperna & Finkelman, 1993 have a very special character, i.e. two paracloacal protuberances in the males; the other adult characters are the same as those of the first group.

– The species from the Cordylidae in South Africa, *M. ineichi* Bain, Wanji, Petit, Paperna & Finkelman, 1993, of which the female is unknown, is distinctive in the following characters: cuticularised buccal capsule, no atrophy of the head papillae (four external labial and four cephalic papillae), long tail, eight pairs of precloacal papillae, oesophagus and spicules longer than in our specimens despite having a smaller body, and smaller microfilariae without a refringent corpuscle and without a swollen caudal extremity. The infective larva is like that of our material (Bain et al., 1993).

– The two species parasitic in the Gekkonidae of the Mediterranean subregion, *M. ivashkini* (Annaev, 1976) in Turkmenistan and *M. wanjii* Bain, Petit, Paperna, Finkelman & Killick-Kendrick, 1992 in Israel, resemble our specimens by the long tail of the male with two pairs of postcloacal papillae and by the post-oesophageal position of the vulva; the sensorial system of the head, when studied, shows an atrophy of the cephalic papillae (*M. wanjii*). However, these two species can be distinguished from our material by the following features: three pairs of precloacal papillae instead of four; oesophagus twice as long; and microfilariae without a refringent corpuscle and a tapering posterior end, especially in *M. ivashkini* (in Reznik, 1982). The infective larvae of *M. ivashkini* are thinner (12–13 μm) and have a shorter tail (18–21 μm, Reznik, 1982); those of *M. wanjii* are also slightly thinner (14–15 μm) but have a longer tail (37-40 μm, Bain et al., 1992). The parasite of *Pachydactylus turneri* from Gauteng Province is therefore a new species for which we propose the name *Madathamugadia hiepei* n. sp., named for Prof. em. Dr. med. vet. habil. Dr. h. c. Th. Hiepe, the former Chief-Director of the Institute of Parasitology and Tropical Veterinary Medicine in Berlin-Mitte, with best wishes for his 70th birthday.

Madathamugadia spp. parasitic in the Gekkonidae represent a small line occurring in the Ethiopian Region and Mediterranean subregion. The three species of this line develop in phlebotomines and the infective larvae are almost identical. The clear post-oesophageal position of the vulva is a late acquisition and constitutes a good synapomorphy: the female genital primordium is anterior in the infective stage and still at the level of the oesophageal intestinal junction in the juvenile female.

Although the Cordylidae is a more recent family than the Gekkonidae (in Estes et al., 1988), its parasite (*M. ineichi*) remains the most primitive representative of *Madathamugadia*, but its biology offers no special feature and clearly demonstrates the close relationship between the species.

Of the nine species of *Madathamugadia* so far described, five, including *M. ineichi*, are found on the African continent (Mali, Angola and South Africa) and two in Madagascar. This suggests an Ethiopian origin of the genus.

Acknowledgements

We wish to express our appreciation to the following persons and institutions: Major Phillip Oosthuizen, Dr Salomon Joubert, Mr Brian Harris, Mr Collin Rowles and the private landowners (especially the Buffalo Lodge) for permission to do the field collection in the Hoedspruit Nature Reserve and the Timbavati/Klaserie/Umbabat Private Game Reserves, respectively; Mr Wulf Haacke and Mr Richard Newbery for much help as regards the reptiles; the Department of Nature Conversation, Gauteng Province, and the Department of Environmental Affairs, Northern Province, for the collecting permits; Dr Errol Nevill for helpful suggestions and discussions concerning the intermediate host; Dr Torsten J. Naucke for the identification of the wild caught sandflies; and Prof. R. Killick-Kendrick for the translation of the manuscript.

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Onderstepoort Journal of Veterinary Research, 69:7–29

Redescription of some *Spauligodon* spp. and *Parapharyngodon* spp., and of *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968 (Pharyngodonidae: Oxyuroidea) from insectivorous South African lizards

S.F.B.N HERING-HAGENBECK[1], A.J. PETTER[2] and J. BOOMKER[3]

ABSTRACT

HERING-HAGENBECK, S.F.B.N., PETTER, A.J. & BOOMKER, J. 2002. Redescription of some *Spauligodon* spp. and *Parapharyngodon* spp., and of *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968 (Pharyngodonidae: Oxyuroidea) from insectivorous South African lizards. *Onderstepoort Journal of Veterinary Research*, 69:7–29

As part of a study on the helminth parasites of South African lizards several species of saurians were collected from localities in the North West Province, the Northern Province, Mpumalanga Province and Gauteng Province. *Spauligodon blydeensis* (Hering-Hagenbeck, 2001) from the Cape thick-toed gecko, *Pachydactylus capensis, Spauligodon molopoensis,* (Hering-Hagenbeck, 2001) from Wahlberg's velvet gecko, *Homopholis wahlbergii, Parapharyngodon margaritiferi,* Hering-Hagenbeck, 2001 from the skink, *Mabuya margaritifer, Parapharyngodon gerrhosauri,* Hering-Hagenbeck, 2001 from the plated lizard, *Gerrhosaurus flavigularis* and *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968 from the skinks *Mabuya punctatissima, Mabuya spilogaster* and *Mabuya varia* are redescribed.

The different *Spauligodon* spp. in the subcontinent may be separated on the presence or absence of spicules in the males, the presence or absence of spines on the tail of both the males and females, as well as on the size and shape of the eggs, and the configuration of the polar caps.

The *Parapharyngodon* spp. are distinguished mainly by the morphological characters of the males, such as the width of the caudal alae and the size of the pre- and adanal papillae. Female *Parapharyngodon* spp. closely resemble each other and some could not be identified to the species level since males were absent.

Spinose larvae, together with adult *Parapharyngodon* spp. were recovered from *Mabuya margaritifer.* All *Parapharyngodon* spp. larvae described to date are spinose and since the larvae in this study were collected together with adult *Parapharyngodon* spp., we consider them to belong to the same genus.

Skrjabinodon mabuyae differs from the closely related *Skrjabinodon mabuiensis* in the presence of a spicule in the male and lateral alae in the female. The former nematode is described for the first time from skinks in South Africa.

Keywords: Gekkonidae, Gerrhosauridae, *Gerrhosaurus, Homopholis, Mabuya,* Nematoda, Oxyuroidea, *Pachydactylus, Parapharyngodon,* Pharyngodonidae, Sauria, Scincidae, *Skrjabinodon,* South Africa, *Spauligodon*

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INTRODUCTION

In total there are approximately 6 550 species of reptiles, of which 480 occur in South Africa. The country is considered to have the highest reptile diversity in Africa, with an average of one new reptile species being described every 44 days (Branch 1998). Surprisingly little information, however, as regards the parasites of these reptiles is available. Reports are few and are generally limited to the description of a new species from a single host or occasionally a small number of hosts, or new host records for some well-known parasites.

Recently, some publications on the helminths of several lizard species in the Western and Northern Cape Provinces have appeared (Bursey, McAllister & Freed 1997; Goldberg & Bursey 2001). The helminths occurring in Turner's thick-toed gecko, *Pachydactylus turneri*, and the skink *Mabuya spilogaster*, as well as a checklist of the helminths of South African snakes and lizards have also been published (Hering-Hagenbeck & Boomker 1998, 2000; Hering-Hagenbeck, Boomker, Petit, Killick-Kendrick & Bain 2000; Hering-Hagenbeck, Boomker & Bain 2001).

As part of a study of the helminth parasites of South African reptiles several species of Sauria were collected from various localities in the northern part of the country. A number of new pharyngodonid nematode species were recovered from the plated lizard *Gerrhosaurus flavigularis*, the Cape thick-toed gecko *Pachydactylus capensis*, Wahlberg's velvet gecko, *Homopholis wahlbergii* and the skinks *Mabuya punctatissima*, *Mabuya spilogaster*, *Mabuya varia* and *Mabuya margaritifer*. The helminth species were described and named by Hering-Hagenbeck (2001) and the purpose of this paper is to validate the new species. Some names are emended to comply with the rules of the International Committee for Zoological Nomenclature and are so indicated.

MATERIALS AND METHODS

The study was conducted in the Molopo Nature Reserve, the campus of the Medical University of Southern Africa, the government farm 'Delftzyl', the Hoedspruit Nature Reserve, the Timbavati, Klaserie and Umbabat complex of private nature reserves and the Blyde River Canyon Nature Reserve, all in the northern regions of the country.The exact localities, as determined by GPS-reading, are provided with the description of each species. The biogeography of each of the study areas has been described by Hering-Hagenbeck (2001), and the vegetation type of each locality by Acocks (1988), Nel, Dell & Newbery (1998) and Low & Rebelo (1996).

The lizards were collected in several ways. The most successful was a modified funnel trap-line, but many specimens were collected by hand by either stunning them with elastic bands or catching them with a butterfly net.

The reptiles were transported live to the laboratory were they were euthanased and their helminths collected, fixed and preserved according to standard procedures. The helminths were placed in a 50 % lactophenol-water solution and examined under a compound microscope while clearing.

Drawings were made with a drawing tube and measurements derived from the drawings. Unless stated otherwise, all measurements are given in millimetres (mm). Measurements are those of the holo- and/or allotype, and, when available, followed by those of the paratypes (in parentheses). Where sufficient material was available specimens were dissected or sectioned to study the spicules, the apical region and transverse sections of the body. Larval stages were identified on the development and the degree of differentiation of the reproductive organs (Jones 1995).

Specimens for scanning electron microscopy were prepared using the techniques of Crang & Klomparens (1995), Dykstra (1992), Robenek (1995) and Flegler, Heckman & Klomparens (1995). The specimens were dehydrated in graded alcohol, critically point dried, sputter coated with gold and examined with a Leica Stereoscan 420 scanning electron microscope at an accelerating voltage of 5kV.

RESULTS AND DISCUSSION

CHARACTERIZATION OF THE GENUS *SPAULIGODON* SKRJABIN, SCHIKHOBALOVA & LAGODOVSKAJA, 1960

TYPE SPECIES: *Spauligodon extenuatus* (Rudolphi, 1819) Skrjabin, Schikhobalova & Lagodovskaja, 1960

Pharyngodonidae with a triangular mouth opening, each lip partially or completely divided into two. Excretory pore posterior to the bulbus, in females always near the vulva. Bulbus with a well-sclerotized valvular apparatus. Lateral alae present. Caudal papillae of males clearly separated into precloacal, adcloacal and postcloacal pairs. Caudal alae not supported by the last pair of genital papillae, the latter being well-separated from each other and usually only a short distance from the adcloacal pair. The protruding genital cone may be supported by sclerotized structures, but the pre- and adcloacal pairs of papillae are never situated on the cone. Spicules are often absent. The usually long and tapering tail may be spinose or aspinose (Skrjabin, Schikhobalova & Lagodovskaja 1960; Petter & Quentin 1976). Parasites of carnivorous reptiles.

Redescription of the species *Spauligodon molopoensis* (Hering-Hagenbeck, 2001) (emended) (Fig. 1 and 2)

Lateral alae are present in both sexes and the nerve ring is situated in the anterior half of the oesophagus, posterior to the commencement of the lateral alae. A conspicuous excretory pore consisting of a transverse slit surrounded by a chitinous rim is present posterior to the bulbus. The tail is long, flexible and, in both sexes, armed with conspicuous cuticular spines.

MALE (*n* = 11) (Fig. 1)

The worms are 2.01 (1.92–2.04) long and 0.15 (0.14–0.16) wide at mid-body. Three lips surround a triangular mouth opening. Each lip is incompletely divided in two lobes. Four cephalic papillae and two lateral amphids are present. Narrow lateral alae start 0.05 (0.05–0.07) from the apex. They are 1.71 (1.59–1.71) long, of more or less uniform width and only widen towards the posterior end. In cross-section the alae carry 6–7 serrations that are not supported by underlying structures (Fig. 1E & E').

The clavate corpus is 0.19 (0.19–0.20) long, the isthmus is 0.02 (0.01–0.02) long, and the almost round bulbus is 0.06 (0.05–0.06) long and 0.07 (0.06–0.07) wide. The nerve ring and excretory pore are situated 0.07 (0.07–0.12) and 0.59 (0.54–0.59) from the anterior end, respectively.

Narrow caudal alae with finely sculptured inner surfaces commence immediately behind the lateral alae. There are three pairs of caudal papillae of which one pair is situated pre-cloacal, one pair adcloacal and one pair post-cloacal. The last-named pair is situated posterior to the caudal alae. The prominent genital cone is surrounded by an ornate, folded membranous lip (Fig. 1I). The weakly sclerotized, V-shaped spicule measures 0.06, with a maximum width of 0.01. The tail is 0.25 (0.17–0.24) long and armed by 6–9 cuticular spines.

FEMALE (*n* = 11) (Fig. 2)

Females are 3.42 (3.02–3.42) long and 0.25 (0.19–0.25) wide at mid-body. The triangular mouth opening is surrounded by three well-developed lips. Each lip carries two papilla-like structures. Cephalic papillae were not seen. The narrow lateral alae start 0.10 (0.09–0.13) from the apex, and are 2.54 (2.15–2.46) long; their outer edges are bilobed (Fig. 2E).

The corpus of the oesophagus is 0.24 (0.23–0.24) long, the isthmus 0.03 (0.03–0.04), and the bulbus 0.10 (0.09–0.10) long and 0.11 (0.11–0.09) wide. The nerve ring and excretory pore are situated 0.10 (0.08–0.12) and 0.41 (0.40–0.43) from the anterior end, respectively. The vulva is slightly posterior to the excretory pore, 0.45 (0.45–0.48), from the anterior end.

The short muscular ovejector together with the common uterus are 0.28 (0.27–0.28) long in total. Two uteri, both running posteriorly for the first third and then diverging into opposite directions, are present. The total length of the uteri is 0.86 (0.85–1.03). Thin-shelled eggs in the uterus measure 0.12 x 0.041; they are elongately ellipsoid with caps on each truncated end and unsegmented when laid. The flexible, filiform tail is 0.96 (0.83–1.11) long, with 10–12 cuticular spines.

TYPE HOST

Pachydactylus capensis (Gekkonidae) 758/II.

TYPE LOCALITY

Molopo Nature Reserve (25°42'48.1"S; 22°48'29.1"E), North West Province, Republic of South Africa.

TYPE MATERIAL

The holotype male, allotype female, ten paratype males and ten paratype females have been deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 276HS.

HABITAT

Large intestine.

ETYMOLOGY

The species is named after the locality of the host.

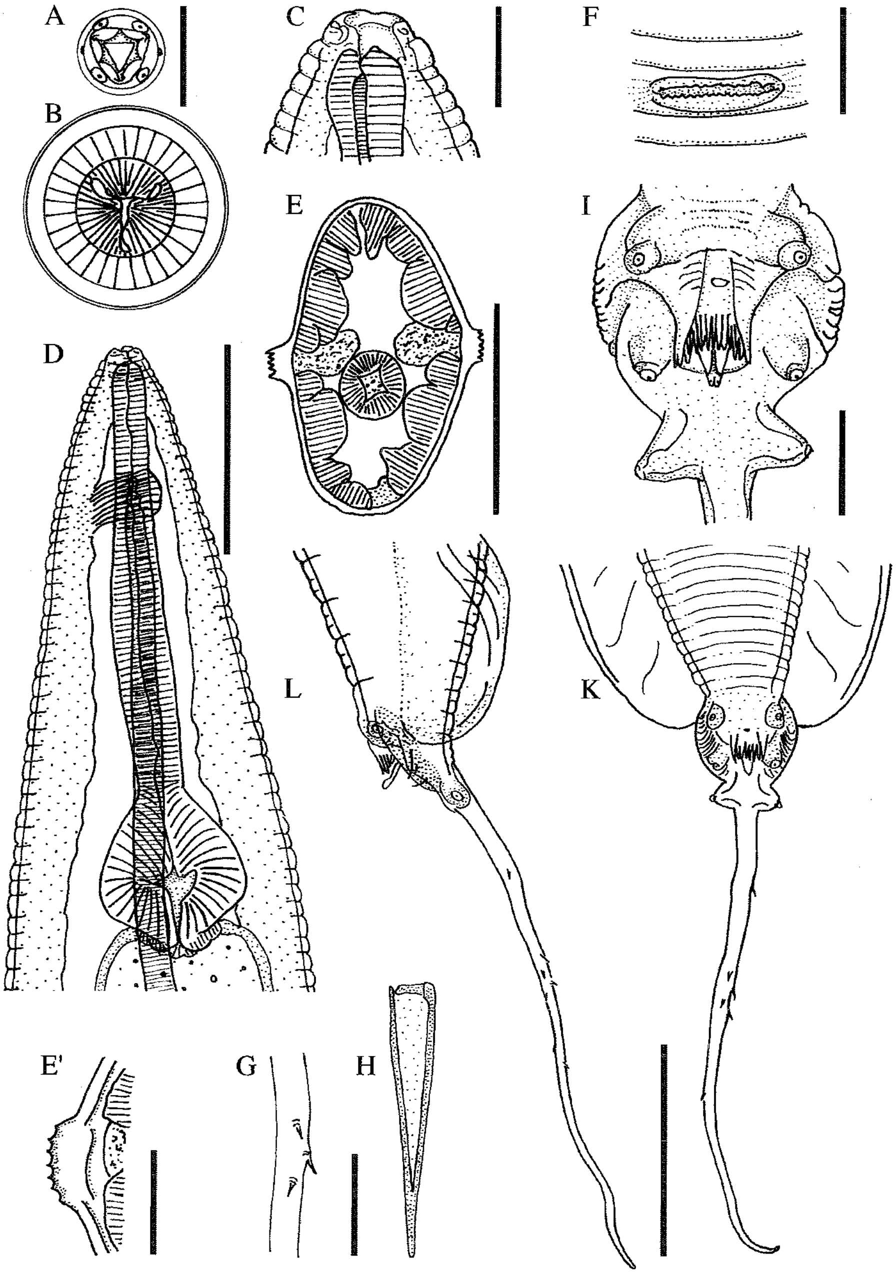

FIG. 1 *Spauligodon molopoensis*, paratype male

- A Apical view of the head
- B Transverse section of the head, 0.02 mm below the apex
- C Median view of the anterior part
- D Lateral view of the anterior part, showing the beginning of the lateral alae
- E Transverse section at mid-body
- E' Higher magnification of a lateral ala showing the serrations
- F Lateral view of the excretory pore
- G Detail of spines on the tail
- H Lateral view of the spicule
- I Ventral view of the genital cone and genital papillae
- K Ventral view of the posterior end
- L Lateral view of the posterior end

Scale bars: A, B, C,E', F, G, H—0.02 mm; D, E, I, K, L—0.1 mm

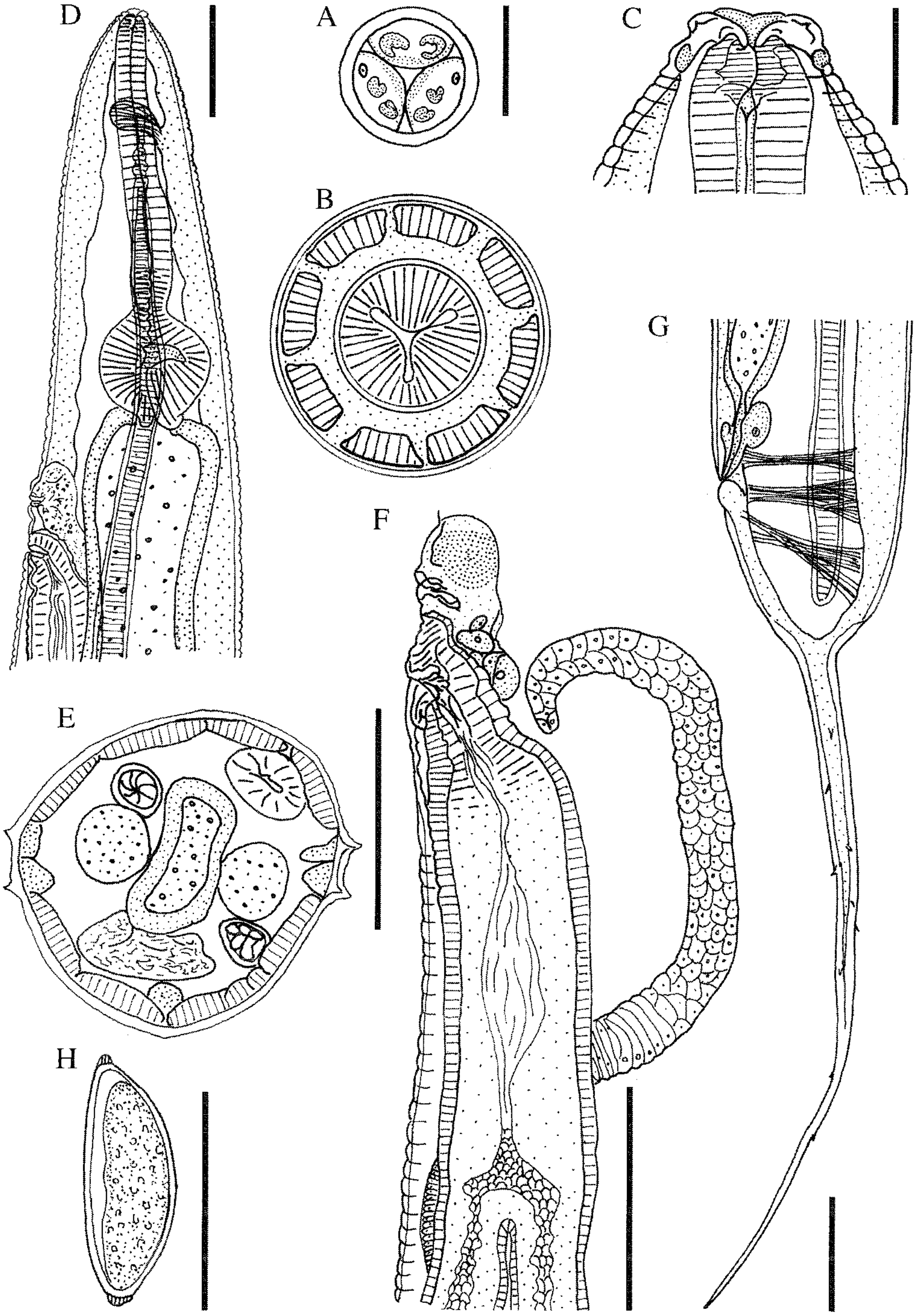

FIG. 2 *Spauligodon molopoensis*, paratype female

A Apical view of the head
B Transverse section of the head, 0.02 mm below the apex
C Median view of the anterior part
D Lateral view of the anterior part showing the beginning of the alae, as well as the excretory pore and vulva
E Transverse section at mid-body
F Lateral view of the vulva and excretory pore
G Lateral view of the posterior end
H Egg

Scale bars: A, B, C—0.02 mm; D, E, F, G, H—0.1 mm

Spauligodon blydeensis **(Hering-Hagenbeck, 2001) (emended)** (Fig. 3 and 4)

Lateral alae present in both sexes. The conspicuous excretory pore is a transverse slit surrounded by a chitinous rim, always posterior to the bulbus. The tail is long, flexible and, in both sexes, armed with conspicuous spines.

MALE (*n* = 2) (Fig. 3)

The holotype male is 2.36 long (paratype damaged) and 0.23 (0.22) wide at mid-body. The triangular mouth opening is surrounded by three sharply pointed lips. Cephalic papillae were not seen. Two prominent amphids occur on the lateral edges of the apex. Distinct lateral alae arise at 0.07 (0.09) from the anterior end, are 1.78 (1.74) long, and of more or less uniform width, only widening towards the posterior end. Just posterior to the bulbus, the alae, in cross section, are 0.02 high and approximately 0.02 wide. They have ten serrations without underlying support (Fig. 3D).

The inner margin of the oesophagus is symmetrical and strongly chitinized. The clavate corpus is 0.29 (0.26) long, the isthmus 0.02 (0.03), and the almost

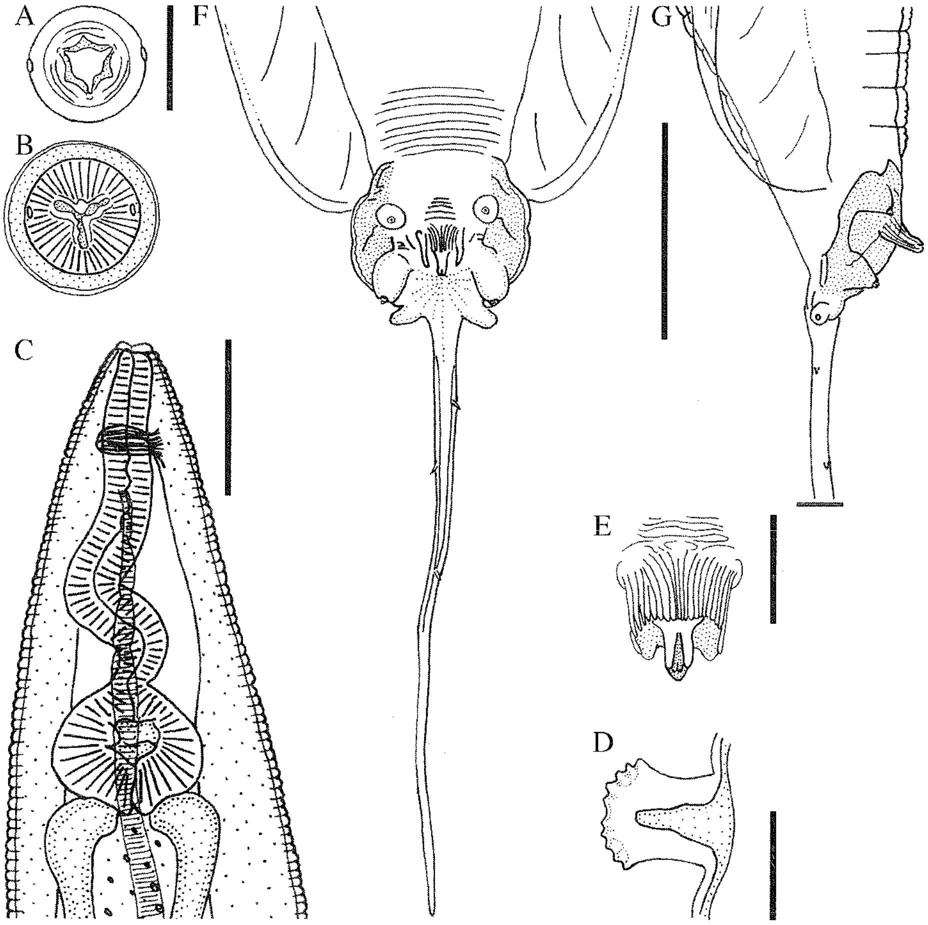

FIG. 3 *Spauligodon blydeensis*, paratype male

- A Apical view of the head
- B Transverse section of head, 0.02 mm below the apex
- C Lateral view of the anterior part with the beginning of the lateral alae
- D Transverse section of a lateral ala, showing the serrations
- E Ventral view of the genital cone
- F Ventral view of the posterior end
- G Lateral view of the posterior end

Scale bars: A, B, D, E—0.02 mm; C, F, G—0.1 mm round bulbus is 0.09 (0.07) long and 0.08 (0.08) wide. The nerve ring and excretory pore are situated 0.06 (0.06) and 0.64 (0.65) from the anterior end, respectively.

Narrow caudal alae commence immediately behind the lateral alae. Three pairs of caudal papillae are present, one pair pre-cloacal and two pairs post cloacal, the posterior pair of which is situated behind the caudal alae.

The prominent genital cone is surrounded by an ornate, folded membranous lip (Fig. 3E). On the tip of the genital cone two minute papilla-like structures are present. A spicule was not seen. The tail is 0.40 long (paratype without tail) and armed by four cuticular spines.

FEMALE ($n = 4$) (Fig. 4)

The females are 1.92 (1.83–2.19) long and 0.19

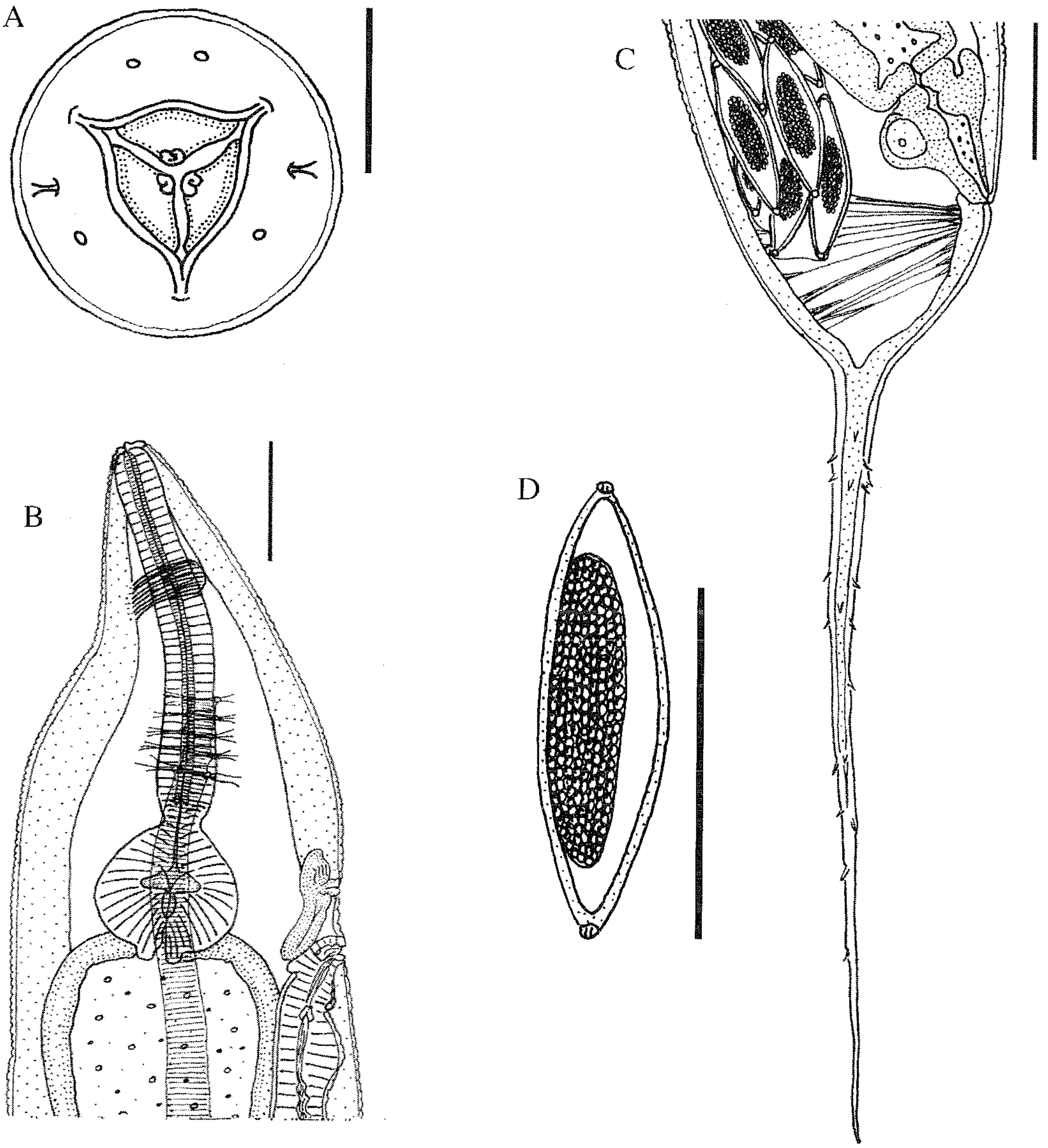

FIG. 4 *Spauligodon blydeensis*, female

A Apical view of the head
B Anterior part showing the beginning of the alae, as well as the excretory pore and vulva, lateral view
C Lateral view of the posterior end, with eggs in the uterus
D Egg

Scale bars: A—0.02 mm; B, C, D—0.1 mm

(0.15–0.17) wide at mid-body. Three prominent, well-developed lips surround a triangular mouth opening. Minute ornamentation is present on the apex of each lip. There are four outer cephalic papillae of which two are situated dorsally and two subventrally. An amphid is present on each side. Narrow lateral alae start 0.22 from the apex, run parallel to the long axis of the body and end just anterior to the anus. The outer borders consist of two prominent expansions, 0.03 apart.

The corpus of the oesophagus is 0.37 (0.39–0.40) long, the isthmus 0.02 (0.01–0.02), and the bulbus 0.13 (0.13–0.14) long and 0.15 (0.14–0.15) wide. The nerve ring and excretory pore are situated 0.12 (0.12–0.15) and 0.41 (0.47–0.53) from the apex, respectively. The vulva is posterior to the excretory pore, 0.47 (0.55–0.62) from the anterior end.

A short muscular ovejector and two uteri are present, the latter running posteriorly, slightly extending beyond the level of the anus. Thin-shelled eggs measure 0.132 x 0.038 *in utero*. They are elongately ellipsoid in shape, with small caps on each sharply truncated end, and unsegmented when laid. The flexible, filiform tail is 0.40 (0.38–0.39) long, with 17–20 prominent cuticular spines.

TYPE HOST

Homopholis wahlbergii (Gekkonidae) 740/II.

TYPE LOCALITY

Blyde River Canyon Nature Reserve (24°40'15.4"S; 30°48'48.0"E), Mpumalanga Province, Republic of South Africa.

TYPE MATERIAL

The holotype male, allotype female, paratype male and three paratype females are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 277HS.

HABITAT

Large intestine.

ETYMOLOGY

The species is named after the locality of the host.

Discussion

Only in the genera *Pharyngodon* Diesing, 1861, *Skrjabinodon* Inglis, 1968 and *Spauligodon* Skrjabin, Schikhobalova & Lagodovskaja, 1960, does the vulva open just behind the post-bulbar excretory pore in the anterior part of the body. In contrast to the males of *Pharyngodon*, which have well-developed caudal alae enveloping all genital papillae, *Skrjabinodon* males lack the caudal alae, while the males of *Spauligodon* have caudal alae that do not enclose the posterior pair of papillae.

The most important factor in identifying reptilian oxyurids is their geographical distribution and the identification of their hosts, to at least the family level (Chabaud & Brygoo 1962; Bursey *et al.* 1997; A.G. Chabaud, personal communication 1999). Currently there are 34 species of *Spauligodon* that are separated mainly on the presence or absence of spines on the tail and the shape of the eggs (Bursey & Goldberg 1995). Only five *Spauligodon* species have as yet been described from the Ethiopian region (Table 1).

The males of *S. molopoensis* and *S. blydeensis* are very similar in appearance to *Spauligodon morgani* (Fitzsimmons, 1961), especially as regards the small, almost round, posterior body extremity, the caudal alae, the genital papillae and the genital cone. However, they differ distinctly in the width of the lateral alae, which widen progressively in *S. morgani*, but are almost of a uniform width until they reach the posterior fifth of the body in *S. molopoensis* and *S. blydeensis*. Furthermore, *S. morgani, Spauligodon dimorpha* (Chabaud & Brygoo, 1962) and *Spauligodon petersi* Bursey, McAllister & Freed, 1997 lack spicules and except for *S. morgani* they have aspinose tails. *Spauligodon molopoensis* is currently the only African species that has a spicule and a spinose tail. The males of *S. blydeensis* differ from the other species occurring on the continent by the few (four) spines on the tail and in having by far the longest tail. The host and locality of *Spauligodon smithi* Bursey, McAllister & Freed, 1997 is very similar to that of *Spauligodon timbavatiensis* Hering-Hagenbeck & Boomker, 1998, *S. molopoensis* and *S. blydeensis*. The most conspicuous difference is that the adcloacal pair of papillae is bifid in *S. smithi*.

There are few differences between the females of the African *Spauligodon* spp. *Spauligodon molopoensis* differs only slightly from *S. timbavatiensis*, *S. smithi* and *S. morgani* in the position of the vulva and the excretory pore. *Spauligodon dimorpha* and *S. petersi* are the only ones with an aspinose tail. The females of *S. blydeensis* differ distinctly from the rest by having the largest number of spines on the tail.

TABLE 1 Comparative measurements of the five Ethiopian species of *Spauligodon*

Species	*Spauligodon petersi*	*Spauligodon morgani*	*Spauligodon dimorpha*	*Spauligodon smithi*	*Spauligodon timbavatiensis*	*Spauligodon molopoensis*	*Spauligodon blydeensis*
Author	Bursey *et al.* 1997	Fitzsimmons 1961	Chabaud & Brygoo 1962	Bursey *et al.* 1997	Hering-Hagenbeck & Boomker 1998	This paper	This paper
Males							
Length	1.203	1.690	1.150	1.710	1.990	1.988	2.163
Width	140	140	190	130	155	153	223
Oesophagus	210	270	350	290	305	275	372
Bulbus	60 x 60	65 x 65	70 x 75	60 x 60	80 x 75	63 x 66	79 x 78
Nerve ring	90	80	130	110	135	98	64
Excretory pore	320	500	620	550	625	564	650
Tail	240	290	180	200	210	252	400
Spicule	–	–	–	90	80	56	–
Spines	Smooth	6 spines	Smooth	Smooth	Smooth	6–9 spines	4 spines
Females							
Length	3.100	4.400	4.300	3.100	2.830	3.181	1.979
Width	300	460	350	380	240	214	170
Oesophagus	340	480	590	320	385	361	556
Bulbus	90 x 100	110 x 110	130 x 130	100 x 100	125 x 130	94 x 101	132 x 149
Nerve ring	110	120	140	110	150	98	129
Excretory pore	480	690	580	290	600	415	470
Tail	460	730	530	580	970	759	391
Vulva	530	760	650	330	620	461	547
Eggs	130 x 40	143 x 35	100 x 41	140 x 48	147 x 33	118 x 41	132 x 38
Spines	Smooth	9–11 spines	Smooth	4–10 spines	5–9 spines	10–12 spines	17–20 spines
Host	*Mabuya sulcata sulcata*	*Mabuya striata*	*Chamaeleo pardalis*	*Pachydactylus bibronii*	*Pachydactylus turneri*	*Pachydactylus capensis*	*Homopholis wahlbergii*
Country	South Africa	Malawi	Madagascar	South Africa	South Africa	South Africa	South Africa

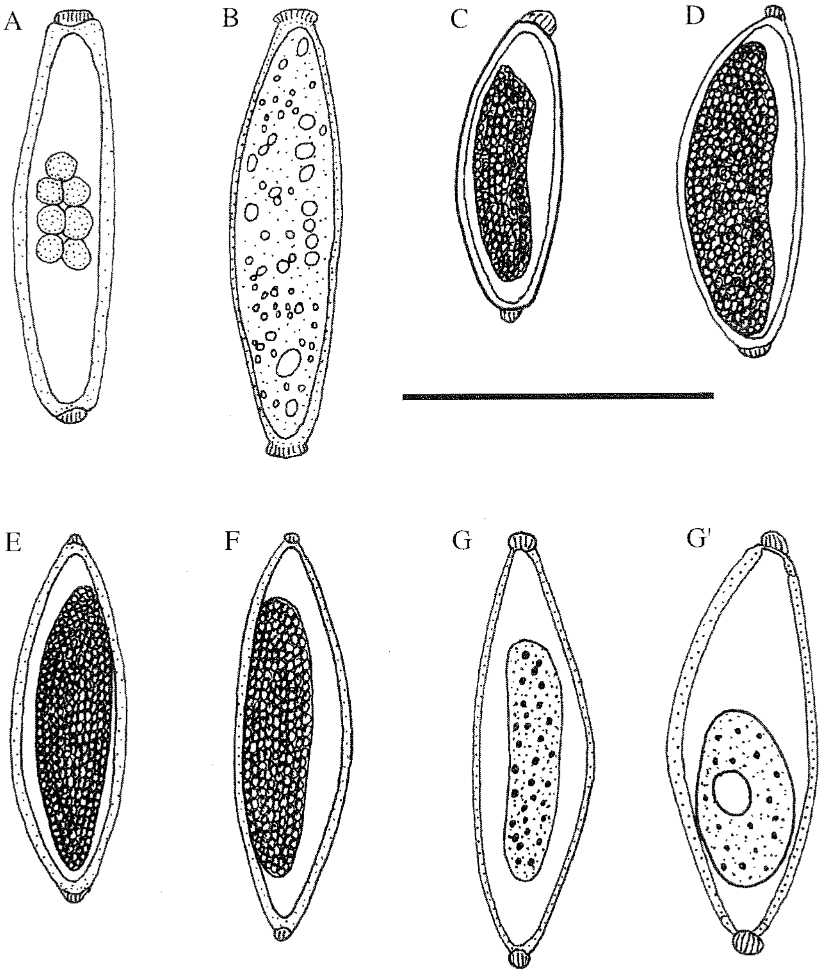

FIG. 5 Eggs of the *Spauligodon* species occurring in reptiles in the Ethiopian region

A	*Spauligodon smithi* (After Bursey *et al.* 1997)
B	*Spauligodon timbavatiensis* (After Hering-Hagenbeck & Boomker 1998)
C	*Spauligodon dimorpha* (After Chabaud & Brygoo 1962)
D	*Spauligodon molopoensis*
E	*Spauligodon petersi* (After Bursey *et al.* 1997)
F	*Spauligodon blydeensis*
G, G'	*Spauligodon morgani* and a variation (After Fitzsimmons 1961)

Scale bar: Bar of 0.1 mm applies to all illustrations

Three characters seem to be of value to distinguish the eggs of the various species, namely the size, the shape and the configuration of the polar caps (Fig. 5). Those of *S. dimorpha* and *S. molopoensis* are the smallest, equal each other in shape, but differ by the arrangement and size of the polar caps. The eggs of *S. petersi*, *S. morgani* and *S. blydeensis* all have the same ellipsoid shape and small, pointed polar caps. However, the caps on the eggs of *S. morgani* are slightly larger and the eggs themselves differ slightly in size. This is also the case for the eggs of *S. timbavatiensis* and *S. smithi*, which are fusiform and truncated, and have large polar caps.

CHARACTERIZATION OF THE GENUS *PARAPHARYNGODON* CHATTERJI, 1933

TYPE SPECIES: *Parapharyngodon maplestonei* (Chatterji, 1933)

Pharyngodonidae with a simple and short buccal cavity and an oesophagus with a typically valved

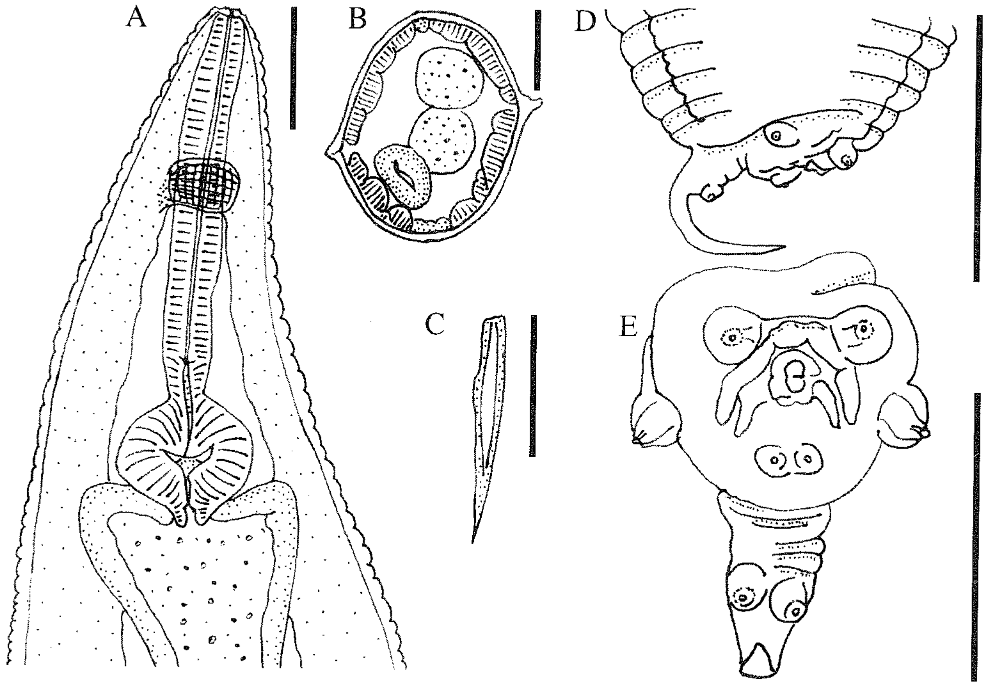

FIG. 6 *Parapharyngodon margaritiferi*, male

A Lateral view of the anterior part
B Transverse section at mid-body
C Spicule in lateral view
D Lateral view of the posterior end
E Posterior end, ventral view

Scale bars: A, B, D—0.1 mm; C, E—0.05 mm

bulbus. Caudal alae are absent in males and the genital cone is absent or reduced. The caudal appendage is truncated immediately posterior to the anus and bears a slim tail. Three to five pairs of mammilliform genital papillae, some of which may be fused, are present, the most posterior pair occurring on the tail. Females are didelphic and prodelphic and the vulva is median. The dorsally curved tail is short and rounded. The eggs have a sub-polar operculum and a thick shell. Parasites of carnivorous reptiles and amphibians (Adamson 1981; Adamson & Nasher 1984).

Redescription of the species *Parapharyngodon margaritiferi* Hering-Hagenbeck, 2001 (Fig. 6 and 7)

Stout, robust nematodes with a thick and distinctly transversely folded cuticle. The cephalic extremity is flattened and the triangular oral opening is surrounded by six prominent elevations. Lateral alae are absent in females.

MALE ($n = 1$) (Fig. 6)

The male is 2.42 long and 0.35 wide at mid-body. The oesophagus is 0.42 long in total. The isthmus is 0.03 long, and the slightly oval bulbus is 0.09 long and 0.11 wide. The intestine is expanded immediately posterior to the bulbus. The nerve ring is situated 0.15 from the apex and the excretory pore 0.74. Lateral alae arise 0.37 from the anterior end and taper off 0.41 from the tip of the tail.

Four pairs of caudal papillae are present, consisting of prominent, mammilliform preanal and adanal pairs, of which the adanal pair lies posterolateral to the anus. Posterior to the genital opening a sessile pair of papillae occurs. The genital cone is minute and surrounded by crescent-shaped and elongated cuticular ornamentation. The spicule pouch opens immediately posterior to the anal opening. The spicule is 0.08 long; the anterior half is of uniform width (0.01), thereafter tapering to a pointed tip. An accessory piece is absent. The crescent-shaped tail is 0.12 long and tapers towards a pointed tip. A

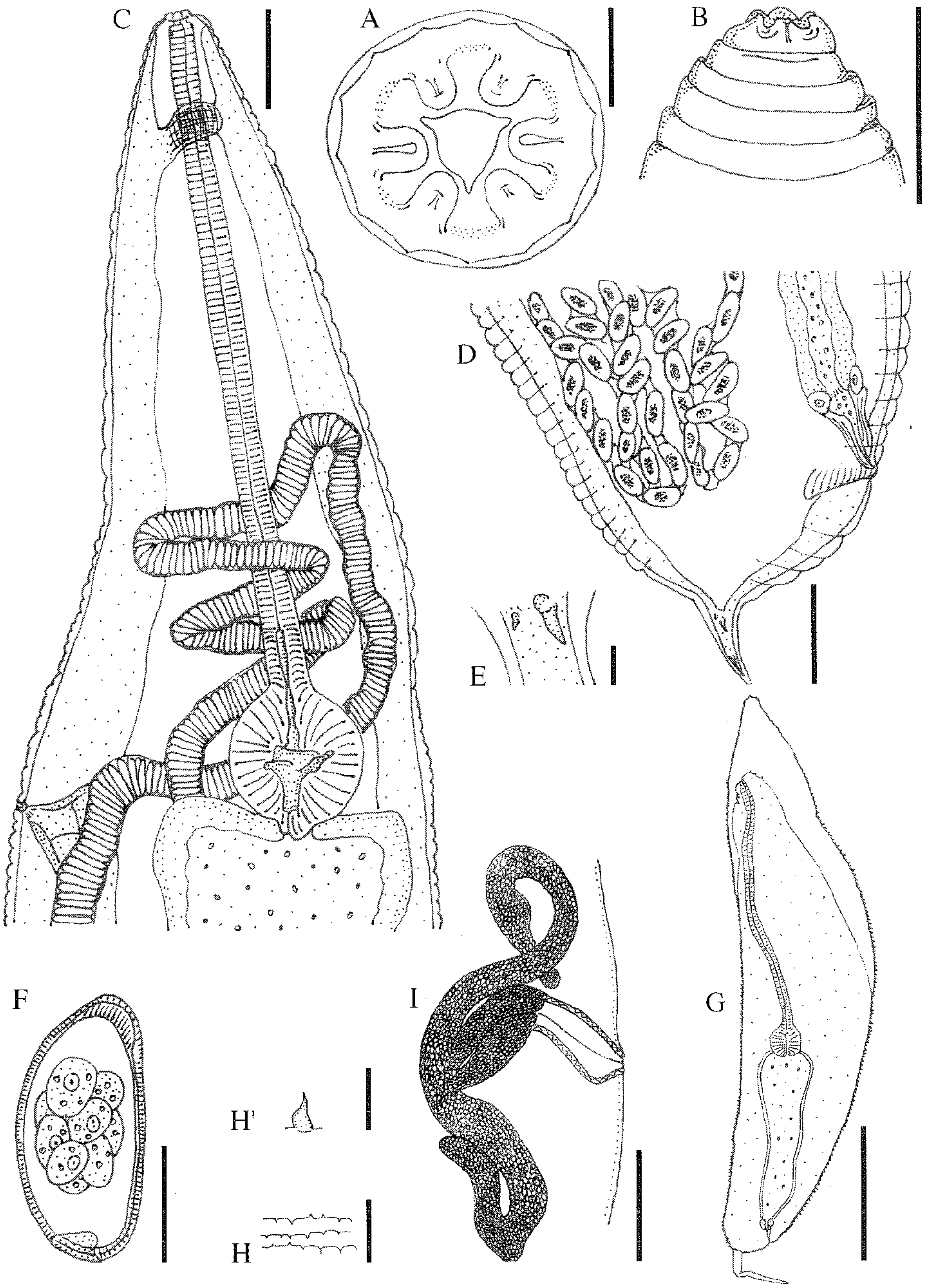

FIG. 7 *Parapharyngodon margaritiferi* female and *Pharyngodon* sp. larva

A Apical view of the head
B Median view of the head
C Lateral view of the anterior part, showing the excretory pore and the anterior uterus loops
D Lateral view of the posterior end
E Details of a spine on the tail
F Egg
G Lateral view of a 3rd stage larva. Note the long oesophagus
H Arrangement of spines on the cuticle of a 3rd stage larva
H' Detail of a cuticular spine of a 3rd stage larva
I Lateral view of the genital primordium of a female 4th stage larva

Scale bars: C, D—0.2 mm; B, I—0.1 mm; F, H, H'—0.05 mm; A—0.02 mm; E—0.01 mm

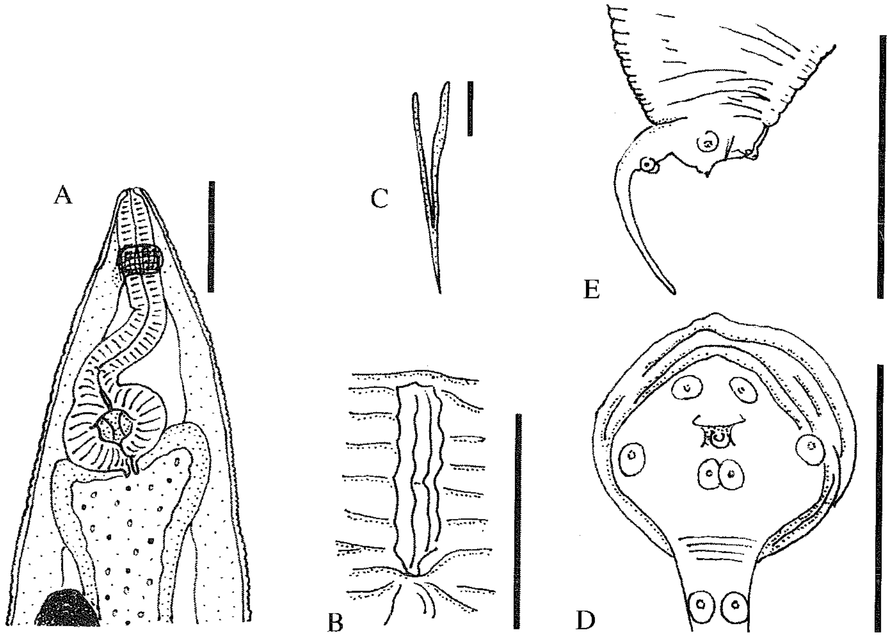

FIG. 8 *Parapharyngodon* sp. no. 1, holotype male

A Lateral view of the anterior part with the cranial part of the testes behind the oesophagus and intestine
B The region where the lateral ala starts in lateral view
C Lateral view of the spicule
D Ventral view of the posterior extremity
E Lateral view of the posterior extremity

Scale bars: A, B, E—0.1 mm; I, D—0.05 mm; H, C—0.01 mm

single pair of papillae is present ventrally in the middle of the tail.

FEMALE (*n* = 2) (Fig. 7)

Length 5.89 (5.27) and width 0.82 (0.87) at midbody. The mouth opening is triangular and surrounded by six prominent rounded elevations, four of which bear a papilla and the other two an amphid each (Fig. 7A). The total length of the oesophagus is 1.62 (1.69). A distinct isthmus is present 1.28 (1.39) from the apex and the bulbus is small and round to slightly oval, 0.29 (0.24) long and 0.29 (0.29) wide. The intestine immediately behind the bulbus is expanded to double the width of the bulbus. The nerve ring is 0.17 (0.22) from the anterior end and the excretory pore is posterior to oesophago-intestinal junction, 1.71 (1.69) from the apex.

The vulva lies more or less at the middle of the body, 3.04 (2.49) from the anterior end. The uterus is didelphic, first running in opposite directions but the posteriorly directed branch later turns anteriorly. The distance from the vulva to the uterus division is 0.85. The uteri are packed with eggs. The ovaries are partly coiled around the oesophagus immediately anterior to the bulbus. The anus is 0.36 (0.44) from the posterior extremity. The tail is orientated slightly dorsally, bearing one prominent and one or two minute spines. Eggs are asymmetrical, rough-shelled, slightly flattened on one side, with subpolar opercula and measure 0.109 x 0.052.

TYPE HOST

Mabuya margaritifer (Scincidae) 856/II.

TYPE LOCALITY

Klaserie Private Game Reserve (24°16'52.4"S; 31° 18'7.3"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male, allotype female and one paratype female are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 278HS.

HABITAT

Large intestine.

ETYMOLOGY

The species is named after the host.

***Parapharyngodon* species no. 1** ($n = 1$) (Fig. 8)

MALE

A small, stout worm 1.69 long and 0.24 wide at midbody. The cuticle is thick and wide transverse striations are present. The total length of the oesophagus is 0.27, that of the isthmus 0.02, and the bulbus is 0.07 long and 0.10 wide. The intestine is slightly expanded posterior to the bulbus. The nerve ring is 0.07 and the excretory pore 0.53 from the anterior end. Lateral alae start at 0.24 from the anterior end and terminate 0.31 from the tip of the tail.

Four pairs of caudal papillae are present. Preanal and adanal pairs are mammilliform and slightly larger than the others. The adanal pair lies posterolateral to the anus. A pair of sessile papillae, situated very close to each other, is present directly posterior to the genital cone. The genital cone is minute, surrounded by two lateral lips and is slightly overlapped by a simple anterior cuticular projection. The spicule pouch opens immediately posterior to the anal opening. The spicule is 0.04 long, with a maximum width of 0.007. It is V-shaped in lateral view. An accessory piece is absent. The thin, crescent-shaped tail is initially directed dorsally, but curves slightly ventrally. It is 0.11 long, tapers to a pointed end and bears a single pair of sessile papillae in the proximal third.

***Parapharyngodon* species no. 2** ($n = 1$)

FEMALE

Apart from the principal measurements, there are no morphological differences between this female and the females of *P. margaritiferi*. The worm is

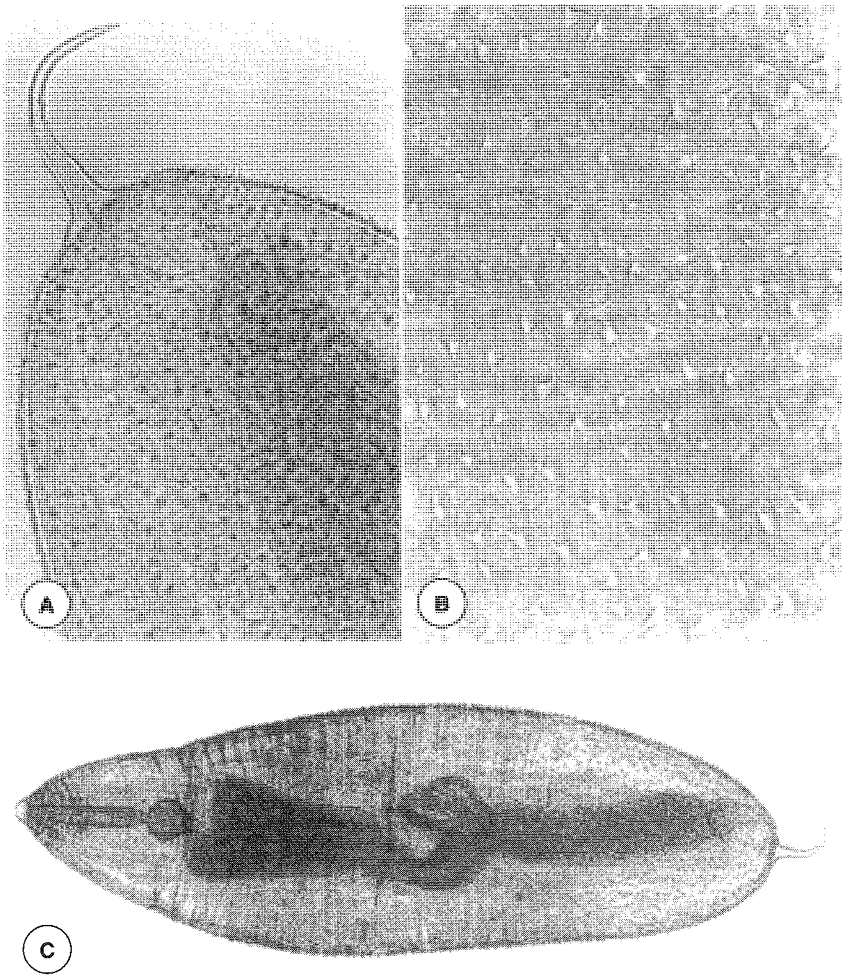

FIG. 9 *Parapharyngodon* spp. third stage larva

A SEM photograph of the posterior part of a 3rd stage larva showing the arrangements of the spines

B Higher magnification of the spines

C Photomicrograph of a 3rd stage larvae in lateral view. Note the short oesophagus

6,44 long and 0.91 wide at mid-body. The oesophagus is 1.42 long and the bulbus is 0.22 long and 0.26 wide. The nerve ring is 0.22 from the anterior end, the excretory pore 1.68 and the vulva 3.22. The tail is 0.36 long.

TYPE HOST

Mabuya margaritifer (Scincidae) 859/2.

TYPE LOCALITY

Klaserie Private Game Reserve (24°16'52.4"S; 31° 18'7.3"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The specimens of *Parapharyngodon* species no. 1 and no. 2 are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 279HS.

HABITAT

Gastrointestinal tract.

Larval stages

Among some hosts infected by the *Parapharyngodon* spp. described above, a few sheathed early 4th stage larvae were recovered.

EARLY STAGE (Fig. 7G, H)

Robust larvae tapering to both ends, 2.50 long and 0.50 wide. The oesophagus is 1.05 long, the bulbus distinct and occurs in the posterior half of the body. Prominent armed transverse striations begin about 0.50 from anterior extremity and continue to the level of the anus. Anterior striations carry 6–8 irregular transverse rows of small conical spines. Posteriorly the spines become larger and more numerous, and in total there are about 74 rows of spines. The latter are either hooked or S-shaped (Fig. 7H and H') and disappear after the 4th moult.

The vulvar primordium lies anterior to the oesophago-intestinal junction, 0.94 from the apex. The vagina is clearly divided into muscular and glandular parts. The muscular vagina is 0.09 long and the divergent uteri divide 0.2 from the vulvar primordium. The posterior uterus is 0.32 long and the ante-

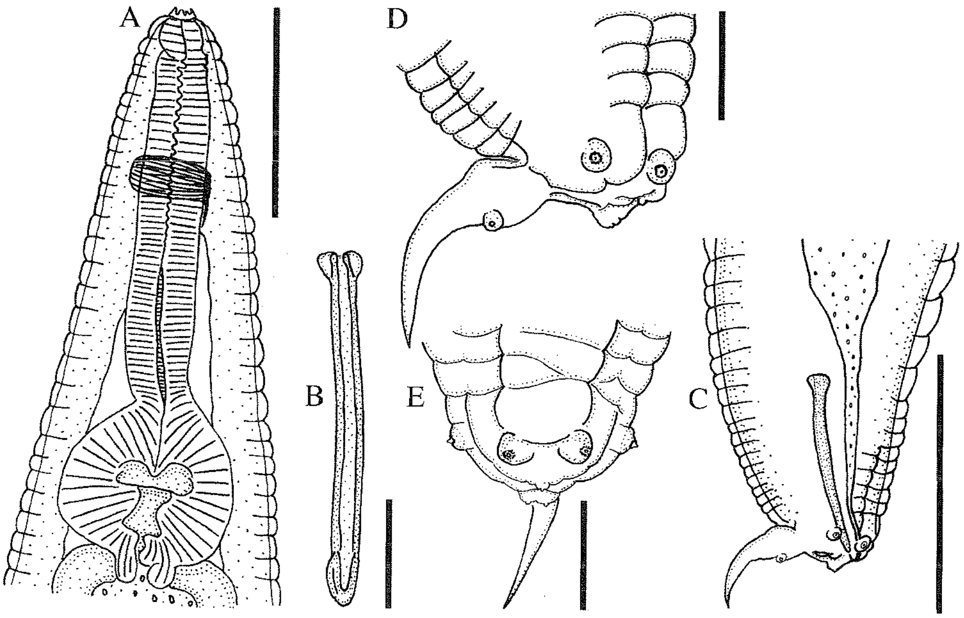

FIG. 10 *Parapharyngodon gerrhosauri*, holotype male

A Median view of the anterior part
B Lateral view of the spicule
C Lateral view of the posterior end showing the position of the spicule
D Lateral view of the posterior end showing the papillae
E Ventral view of the posterior end

Scale bars: A, C—0.1 mm; B, D, E—0.02 mm rior one 0.40, both changing direction in their distal third.

The tail is 0.30 long, unarmed and crescent-shaped. Male larvae were not recovered.

Two more larvae of unknown sex, were in general appearance very similar the one described above, but had a conspicuously short oesophagus (Fig. 7G and Fig. 9C).

LOST

Mabuya margaritifer (Scincidae).

LOCALITY

Klaserie Private Game Reserve (24°16'52.4"S; 31° 18'7.3"E) and Hoedspruit Nature Reserve, Northern Province, Republic of South Africa.

HABITAT

Gastrointestinal tract.

***Parapharyngodon gerrhosauri* Hering-Hagenbeck, 2001** (*n* = 1) (Fig. 10)

MALE

A stout worm, 2.38 long and 0.19 wide at mid-body, with distinct transverse cuticular striations. Oral opening surrounded by six triangular lips. In lateral or ventral view, the cephalic papillae and amphids are not visible. The oesophagus is 0.26 long, the isthmus is indistinct, and the bulbus is almost round, 0.09 long and 0.08 wide. The nerve ring is situated in the anterior third of the oesophagus, 0.08 from the anterior end and the excretory pore 0.85. Lateral alae arise 0.13 from the cephalic extremity and extend to 0.37 from the tip of the tail.

Three pairs of mammilliform caudal papillae are present, one pair preanal, one adanal, posterolateral to the anus, and one pair occurs on the proximal third of the tail. The genital cone is simple, without ornamentation and projections. Posterior to the genital cone a single, minute papilla is present. The

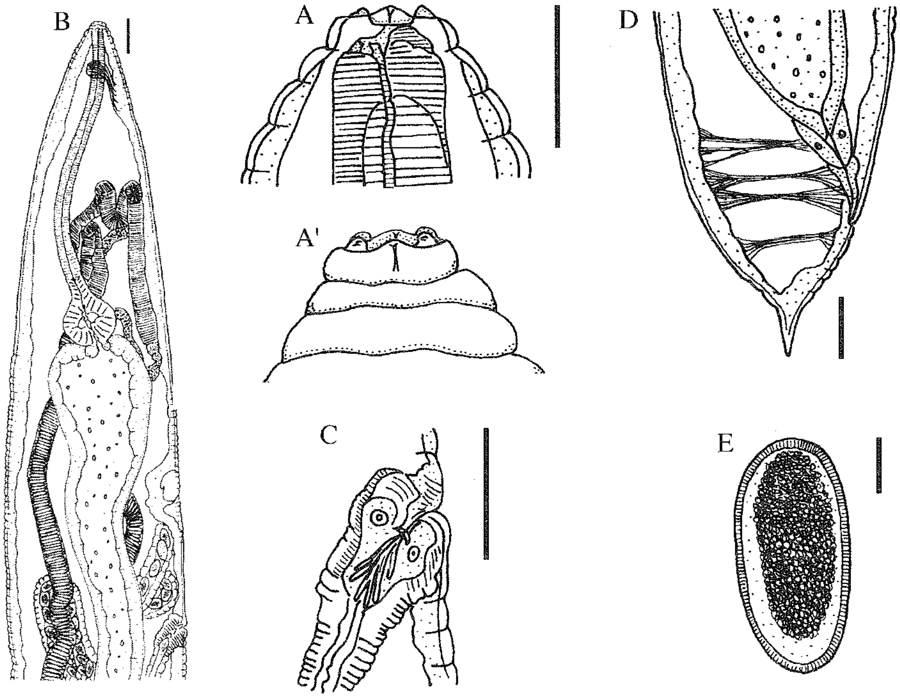

FIG. 11 *Parapharyngodon* sp. no. 3, female

- A, A' Median view of the anterior end
- B Anterior part, showing the position of the excretory pore, the vulva and the cranial parts of the uterus
- C Lateral view of the vulva and ovejector
- D Lateral view of the posterior end
- E Egg

Scale bars: A, A', B, C, D—0.1 mm; E—0.02 mm spicule pouch opens immediately posterior to the anal opening. The spicule is 0.07 long, weakly sclerotized and of almost uniform width (0.005) with a rounded tip. The tail is dorsally directed, crescent-shaped, 0.06 long, and tapers to a pointed tip.

TYPE HOST

Gerrhosaurus flavigularis (Gerrhosauridae) 168/II.

TYPE LOCALITY

Timbavati Private Game Reserve (24°29'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male is deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 280HS.

HABITAT

Large intestine.

ETYMOLOGY

The species is named after the host.

***Parapharyngodon* sp. no. 3** ($n = 1$) (Fig. 11)

FEMALE

Total length 4.29, maximum width 0.56.

Distinct transverse striations occur on the body cuticle between the oesophago-intestinal junction and the rectum, while the remainder of the body is indistinctly striated. The oral opening is surrounded by six prominent lips, the lateral ones of which each bear an amphid. The oesophagus is 0.96 long, the isthmus is distinct and 0.05 long, and the bulbus more or less round, 0.07 long and 0.08 wide. The nerve ring is situated close to the anterior end, 0.08 from the apex, and the excretory pore and vulva 1.44 and 1.78, respectively.

The vulva is prominent, didelphic and prodelphic. Parts of the ovaries are coiled around the oesophagus immediately anterior to the bulbus. The reproductive organs in this specimen were partly destroyed, therefore no further description is possible. Uteri are filled with eggs measuring 0.069 x 0.034 and which seem to be infertile due to the absence of males. An operculum was not observed.

HOST

Gerrhosaurus flavigularis (Gerrhosauridae) 166/II.

LOCALITY

Timbavati Private Game Reserve (24°29'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

MATERIAL

The specimen is deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 281HS.

HABITAT

Large intestine.

Discussion

For many years there have been conflicting views on the taxonomic validity of *Parapharyngodon* (Jones 1992). Although some authors consider the genus as a synonym of *Thelandros* Wedl, 1862 (Baylis 1936; Petter & Quentin 1976; Vincente, Rodrigues, Gomes & Pinto 1993), we regard *Parapharyngodon* as an independent genus as redefined by Adamson (1981). According to Adamson (1981) and Adamson & Nasher (1984), *Thelandros* is readily distinguishable from *Parapharyngodon* by the presence of a prominent genital cone, a marked distance between the anus and the spicule pouch, and the caudal pre- and adanal papillae which are pedunculated in *Thelandros* but mammilliform in *Parapharyngodon*. The eggs of *Thelandros* have terminal opercula and *in utero* already contain a larva. In addition, *Thelandros* is known to occur in omni- or herbivorous reptiles, whereas *Parapharyngodon* is found in insectivorous reptiles and amphibians. These characteristics have been accepted by Baker (1987), Moravec, Barûs & Rysavy (1987), Hobbs (1996) and Moravec, Salgado-Maldonado & Mayen-Peña (1997).

In addition to the several *species inquirendae* (Adamson 1981), which can probably be referred to the genus, more than 30 *Parapharyngodon* species have so far been described (Baker 1987) and the genus can be considered cosmopolitan.

Except for one species which is known from South Africa, namely *Parapharyngodon rotundatus* (Malan, 1939) Freitas, 1957 from *Agama atra* and *Pseudocordylus microlepidotus,* all the African species occur in countries north of the equator. Adamson

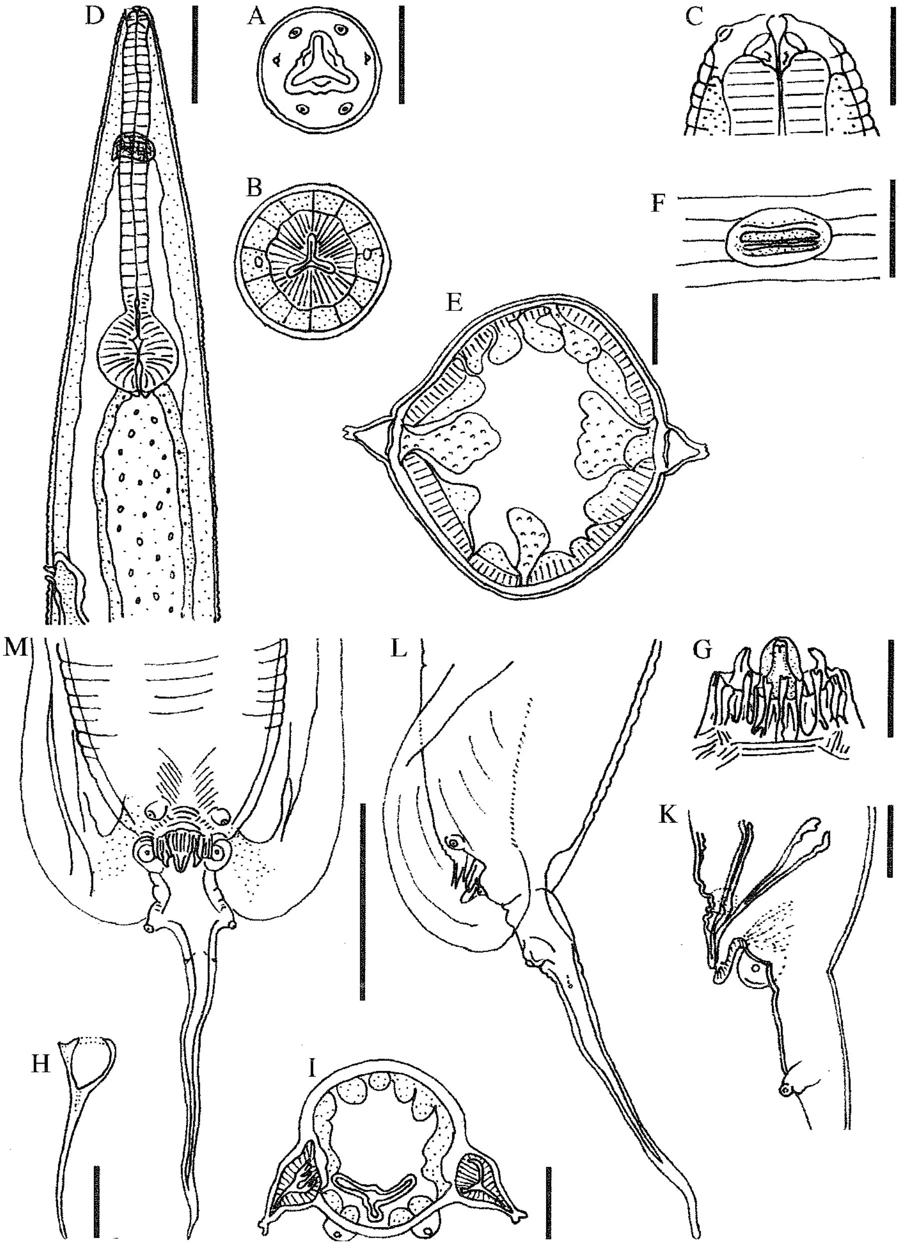

FIG. 12 *Skrjabinodon mabuyae* male from *Mabuya striata*

A Apical view of the head
B Transverse section of the head, 0.011 mm below the apex
C Median view of the head
D Lateral view of the anterior part including the excretory pore
E Transverse section at mid-body
F Ventral view of the excretory pore
G Ventral view of the genital cone
H Lateral view of the spicule
I Transverse section between the anterior pair of genital papillae and the genital cone
K Lateral view of the posterior end showing the position of the spicule
L Lateral view of the posterior end
M Ventral view of the posterior end

Scale bars: D, L, M—0.1 mm; A, B, C, E, F, G, H, I, K—0.02 mm

(1981) and Baker (1987) mistakenly quoted *Parapharyngodon rousseti* (Tcheprakoff, 1966) Adamson, 1981 from *Agama bibronii boneti* as a South African species. Besides the fact that Tcheprakoff (1966) names "In'Ekker, région d'In' Anguel Hoggar" (equivalent to Ahaggar in Algeria) as the host locality, *A. bibronii boneti* does not occur in South Africa.

The males of *P. rotundatus* differ distinctly from our *Parapharyngodon* spp. in having prominent and wide alae. Furthermore, the morphology of the caudal extremity as well as the size of the pre- and adanal papillae differ completely between *P. rotundatus* and the species redescribed here. The latter can be differentiated from each other in that the genital cone of *P. margaritiferi* is surrounded by

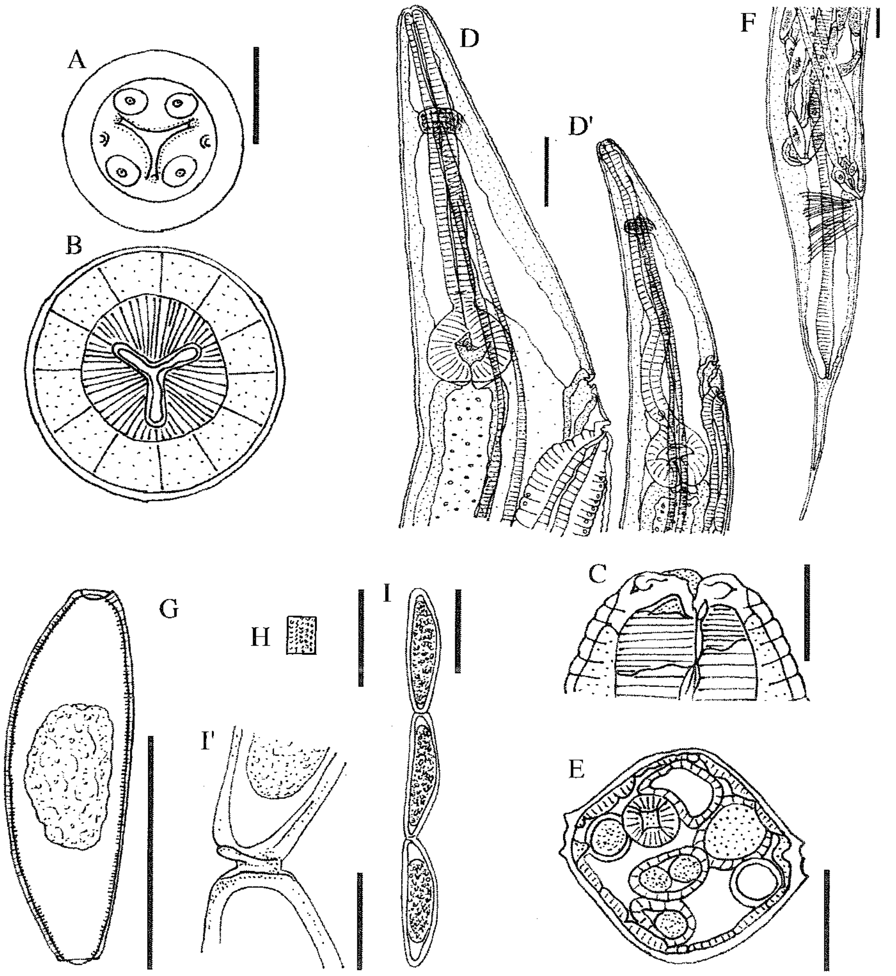

FIG. 13 *Skrjabinodon mabuyae* female from *Mabuya striata*

A	Apical view of the head
B	Transverse section of the head 0.02 mm below the apex
C	Median view of the head
D, D'	Anterior parts of two females of different size, showing the relative position of the of the vulva and excretory pore as well as the beginning of the alae
E	Transverse section at mid-body
F	Lateral view of the posterior end
G	Egg
H	Detail of the egg-shell's surface
I, I'	A string consisting of three eggs and detail of the connection between the eggs

Scale bars: D, D', E, F, G, H, I—0.1 mm; A, B, C, I'—0.02 mm crescent-shaped and elongated cuticular ornamentation, that of *P. gerrhosauri* is simple, without ornamentation and projections, and that of *Parapharyngodon* sp. no. 1 is surrounded by two lateral lips and is slightly overlapped by a simple anterior cuticular projection.

The different species of the genus *Parapharyngodon* are mainly distinguished by morphological characters of the males. The similarity of the females of this genus makes it impossible to distinguish them without accompanying male specimens. For this reason the female from *G. flavigularis* cannot be linked to *P. gerrhosauri* although the host species and collecting area indicate a possibility of the two belonging together.

All *Parapharyngodon* larvae described to date are spinose (Barûs 1973; Adamson & Nasher 1984) and the arrangement of the spines is very similar to that of adult *Indiana* Chakravarty, 1943 (Thelastomatidae: Oxyuroidea), a parasite of insects (Bain 1965). In nematodes the ontogenesis is often expressed in the phylogeny and the larval characters of *Parapharyngodon* strengthen the hypothesis that this nematode genus may be derived from a nematode of insects. According to Blaxter, De Ley, Garey, Liu, Scheldeman, Vierstraete, Vanflenteren, Mackey, Dorris, Frisse, Vida & Kelley (1998) the Oxyuroidea of vertebrates have evolved from arthropod ancestors and Petter & Quentin (1976) presumed the thelastomatids to be the ancestors of the Pharyngodonidae. The spiny cuticle of the *Parapharyngodon* larvae may be a remnant of this ancestry (Adamson & Nasher 1984).

Since the L4-larvae described above were collected together with adult members of the genus, we consider the larvae to belong to the genus *Parapharyngodon*. This identification, however, assumes that spiny larvae are characteristic for the genus.

A detailed description of the developing female reproductive system has so far only been reported by Adamson & Nasher (1984). Contrary to their observations, coelomocytes surrounding each growing ovary were not visible in the *Parapharyngodon* larvae redescribed here, which could be due to advanced larval age. What remains unclear is whether the two different larval forms, distinguishable by the length of the oesophagus, are different sexes or even different species.

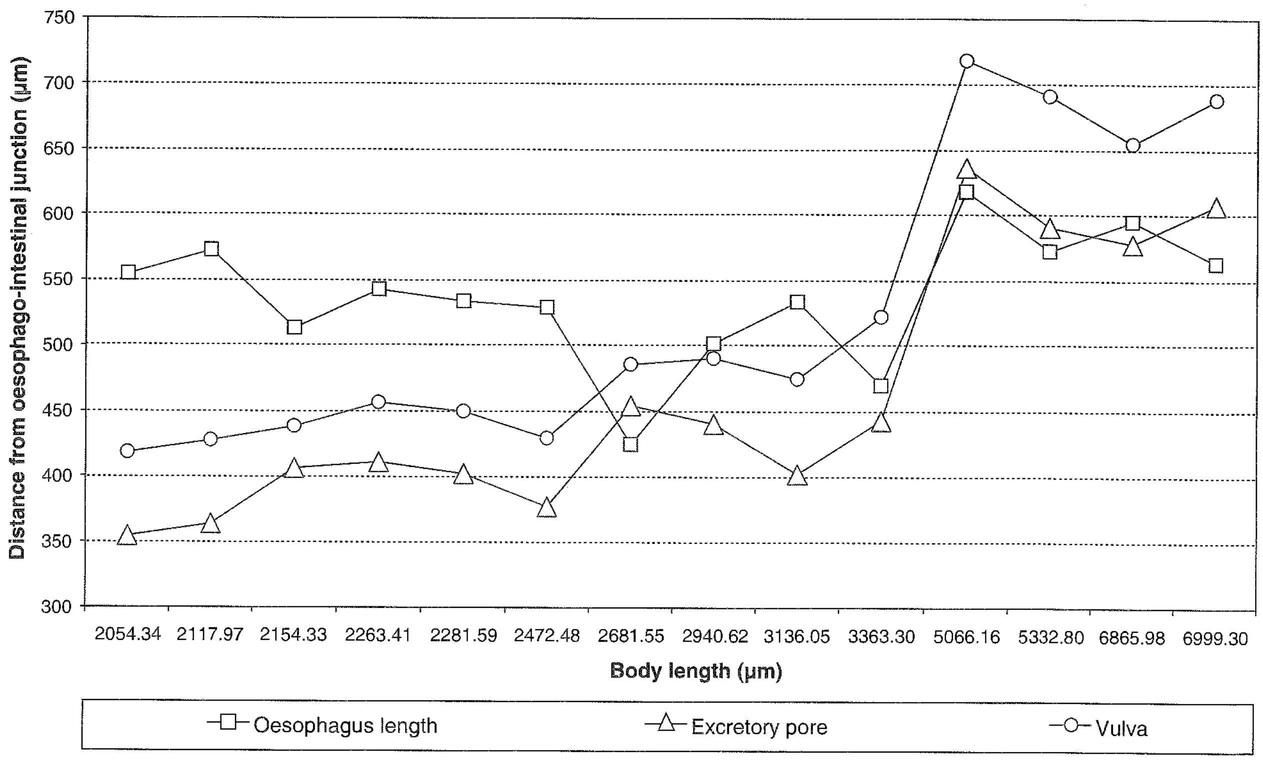

FIG. 14 The relationship between the body length, length of the oesophagus, and the position of the vulva and excretory pore in adult and subadult *Skrjabinodon mabuyae* females

CHARACTERIZATION OF THE GENUS *SKRJABINODON* INGLIS, 1968

TYPE SPECIES: *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968

Pharyngodonidae, with lateral alae frequently very narrow, particularly in females. The mouth opening is bound by three bilobed lips. The tail terminates in a long spike, often barbed in the female. Spicules may be absent. The cloacal region is raised forming a narrow elongated cone. Caudal alae are absent. Two pairs of cloacal papillae are always separate from the cone and one pair of postcloacal papillae is often present near the cloacal pairs. The caudal papillae are sessile and often reduced. Cosmopolitan parasites of reptiles (Inglis 1968; Petter & Quentin 1976).

Redescription of the species *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968

(Fig. 12 and 13)

Cuticle thick and transversely striated. Lateral alae are present in both sexes. The mouth opening is triangular and surrounded by three small lips. There are four more or less conspicuous cephalic papillae. The lateral lips each have one papilla and an amphid, and each of the submedian lips bears one cephalic papilla. The prominent excretory pore is surrounded by a cuticular rim. Lateral alae arise at the level of the nerve ring. A long and thin tail, unarmed in both sexes, is present.

MALE (*n* = 9, from five different hosts) (Fig. 12)

Males are 2.01 (1.35–2.35) long and 0.19 (0.12–0.24) wide at mid-body. The oesophagus is 0.41 (0.37–0.45) long and of uniform width. The bulbus is 0.08 (0.07–0.09) long and 0.09 (0.07–0.10) wide, and the isthmus is 0.29 (0.29) from the cephalic extremity. The alae are 1.75 (1.42–2.07) long and arise 0.13 (0.09–0.15) from the anterior end, near the nerve ring which is situated 0.17 (0.10–0.25) from the apex. The excretory pore lies at the level of the bulbus or slightly posterior to it, 0.54 (0.36–0.61) from the anterior end. In transversal section, the alae are longitudinally grooved, the groove deepening towards the posterior end (Fig. 12E and I).

The caudal papillae are arranged as described by Sandground (1936). The spicule is poorly sclerotized and hardly visible, V-shaped, 0.062 long and 0.017 in maximum width. The tail is 0.22 (0.19–0.25) long.

FEMALE (*n* = 16, from five different hosts) (Fig. 13)

Length 3.62 (2.05–6,99) and width at mid-body 0.23 (0.15–0.38). The total length of the oesophagus is 0.54 (0.43–0.62); the bulbus is 0.10 (0.09–0.12) long and 0.11 (0.09–0.14) wide and the isthmus is 0.43 (0.42–0.45) from the anterior end. Alae arise 0.13 (0.11–0.16) from the anterior end, often anterior to the nerve ring which is situated 0.15 (0.10–0.19) from the apex. The prominent vulva lies 0.52 (0.42–0.72) from the apex, always posterior to excretory pore which is 0.46 (0.36–0.64) from the anterior end. The alae are 3.05 (1.60–6,08) long and configured as in the males, but in transverse section the longitudinal groove is shallower (Fig. 13E).

A well-developed muscular vagina, 0.81 long, leads into a long common uterus which divides 1.26 from the vulva into two uteri that run anteriorly for a short distance and then divert in opposite directions. Ovaries are about 1.87 long. Eggs are asymmetrical, being flattened on one side. They are operculated at both poles, have a rough surface and measure 0.156 (0.142–0.161) x 0.053 (0.051–0.055). Eggs, containing a morula, are laid in long strings (Fig. 13I and I').

In Fig. 14 the variation in the position of the excretory pore and vulva in relation to the oesophago-intestinal junction is shown. As expected, the older (larger) the specimens were, the more posterior the vulva and excretory pore were to the oesophago-intestinal junction.

TYPE HOST

Mabuya varia (Scincidae).

TYPE LOCALITY

Mount Elgon, Uganda.

OTHER HOSTS AND LOCALITIES

Mabuya punctatissima from Delftzyl Government Farm (24°40'39.6"S; 29°14'23.8"E), Northern Province, Republic of South Africa.

Mabuya varia from the Timbavati Private Game Reserve (24°16'52.4"S; 31°18'7.3"E), Northern Province and the Blyde River Canyon Nature Reserve (24°43'5.9"S; 30°50'31.0"E), Mpumalanga Province, Republic of South Africa.

Mabuya punctatissima and *Mabuya varia* from the campus of the Medical University of Southern Africa

(25°36'51.8"S; 28°01'30.5"E), Gauteng Province, Republic of South Africa.

Mabuya spilogaster and *Mabuya punctatissima* from the Molopo Nature Reserves (25°40'–53'S; 22°49'–56'E), North West Province, Republic of South Africa.

TYPE MATERIAL

The type specimens are deposited in the collection of the U.S. Department of Agriculture-Agricultural Research Service (U.S. National Parasite Collection).

OTHER MATERIAL

The specimens collected during this survey are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 282HS.

HABITAT

Large intestine.

Discussion

The genus *Skrjabinodon* was established by Inglis (1968) when revising the genus *Parathelandros* Diesing, 1861, restricting the latter to accommodate only species parasitic in Australian frogs. This has been accepted by a number of authors (Petter & Quentin 1976; Baker 1987; Moravec *et al.* 1987, 1997; Ainsworth 1990; Hornero & Roca 1992). Since Inglis's (1968) revision several of *Parathelandros* spp. have been described from lizards outside Australia, the validity of which was questioned by Baker (1987).

Morphologically and morphometrically our specimens are very close to *S. mabuyae,* differing mainly in host species and host locality. *Skrjabinodon mabuiensis* (Malan 1939) described from *Mabuya striata* in the Western Cape Province differs by the absence of spicules in the males and lateral alae in the females (Malan 1939). Comparison with specimens of *S. mabuiensis* could have excluded the possibility of synopnymy but it was not possible to trace the type specimens and the present specimens are therefore assigned to *S. mabuyae*.

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Onderstepoort Journal of Veterinary Research, 69:31–51

Redescription of some *Thelandros* and *Tachygonetria* spp. (Pharyngodonidae: Oxyuroidea) from the omnivorous plated lizard, *Gerrhosaurus validus validus* A. Smith, 1849 in South Africa

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ABSTRACT

HERING-HAGENBECK, S.F.B.N., PETTER, A.J. & BOOMKER, J. 2002. Redescription of some *Thelandros* and *Tachygonetria* spp. (Pharyngodonidae: Oxyuroidea) from the omnivorous plated lizard, *Gerrhosaurus validus validus* A. Smith, 1849 in South Africa. *Onderstepoort Journal of Veterinary Research,* 69:31–51

Thelandros schusteri Hering-Hagenbeck, 2001, *Thelandros luciusi* Hering-Hagenbeck, 2001, *Thelandros boomkeri* Hering-Hagenbeck, 2001, *Tachygonetria bainae* Hering-Hagenbeck, 2001, *Tachygonetria chabaudi* Hering-Hagenbeck, 2001 and *Tachygonetria petterae* Hering-Hagenbeck, 2001 from the plated lizard, *Gerrhosaurus validus validus* A. Smith 1849 from three localities in the north-eastern region of South Africa are redescribed. Classification keys are available only for the males of the species and because male and female nematodes *in copula* were not observed in this study as well as the similarity of the females, it was not possible to identify the females to the species level. *Thelandros schusteri*, *Thelandros boomkeri* and *Thelandros luciusi* were provisionally paired with female Type E, *Tachygonetria bainae* with female Type C, *Tachygonetria chabaudi* with female Type A and *Tachygonetria petterae* with female Type D. Female Types B and F could not be paired.

The richness and composition of species of the Pharyngodonidae of *Gerrhosaurus validus validus* is close to that of tortoises and differs from the pharyngodonid fauna of the insectivorous lizards that have been studied. In the latter, only the genera *Spauligodon*, *Skrjabinodon* and *Parapharyngodon* were recovered. The pharyngodonid fauna of *Gerrhosaurus validus validus* seems to have originated by capture from local herbivorous reptiles. The three *Tachygonetria* spp. most closely resemble forms in South African tortoises. The three *Thelandros* spp. redescribed here not only show strong similarities to those of herbivorous *Agama* spp., but also to those parasitic in tortoises and could have been acquired from either.

Keywords: Gerrhosauridae, *Gerrhosaurus validus validus*, Oxyuroidea, Pharyngodonidae, South Africa, *Tachygonetria*, *Thelandros*

INTRODUCTION

Gerrhosaurus validus validus is widely spread in the eastern and northern regions of South Africa and also occurs in Mozambique, Malawi and Zimbabwe. The other subspecies, *Gerrhosaurus validus maltzahni* is limited to northern Namibia and southern Angola. *Gerrhosaurus validus validus* is the largest of the genus, attaining a length of about 70 cm. They are rupicolous and largely confined to rocky and boulder-strewn hills and outcrops in arid and mesic savannah habitats (Hering-Hagenbeck

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2001). They hide in cracks from which it is nearly impossible to remove them and they wedge themselves in place by laying the tail around the body and filling the lungs with air. The lizards are highly territorial and live in small family groups. Their food consists of leaves, flowers and fruits but insects, spiders, millipedes, scorpions and small lizards and mammals are also taken (Branch 1998). They wander over a large area in search of food, but when disturbed they run along the quickest route back to their territory.

As part of a study of the helminth parasites of South African reptiles the helminths of *G. validus validus* were collected from various localities in the north-eastern part of the country. The helminths were described and named by Hering-Hagenbeck (2001) and the purpose of this paper is to validate the new species. All the helminths redescribed here are new host records and are also the first helminths to be described from *G. validus validus.*

MATERIALS AND METHODS

The study was conducted in the Hoedspruit Nature Reserve, and the Timbavati and Klaserie complex of private nature reserves, Northern Province, South Africa. The exact localities, as determined by GPS-reading, are provided with the redescription of each helminth species. The biogeography of these areas has been described by Hering-Hagenbeck (2001), and the vegetation type of each by Acocks (1988) and Low & Rebelo (1996).

The lizards were collected and processed for helminth recovery as described by Hering-Hagenbeck, Petter & Boomker (2002). The helminths were placed in a 50 % lactophenol-water solution and examined under a compound microscope while clearing. Drawings were made with a drawing tube and measurements derived from the drawings. Unless stated otherwise, all measurements are given in millimetres (mm). Measurements are those of the holo- and/or allotype, and, when available, followed by those of the paratypes (in parentheses). Where sufficient material was available specimens were dissected or sectioned to study the spicules, the apical region and transverse sections of the body.

RESULTS AND DISCUSSION

CHARACTERIZATION OF THE GENUS *THELANDROS* WEDL, 1862

TYPE SPECIES: *Thelandros alatus* Wedl, 1862

Pharyngodonidae. Cuticle with distinct transverse striations. Females with variable tail characters. Eggs often with a terminal cap, containing a larva when laid. Males with reduced caudal appendages. Genital cone prominent, supported by an anterior anal lip. Four pairs of caudal papillae are present; one pre-anal and one adanal pair of pedunculated rosette papillae, one postanal pair of nerve endings, median on the genital cone and opening into the spicule pouch, and one ventral pair in the middle of the tail. Parasites of herbivorous or omnivorous lizards (Adamson 1981; Adamson & Nasher 1984).

Redescription of the species *Thelandros schusteri* Hering-Hagenbeck, 2001 (Fig. 1)

MALE ($n = 10$)

Length 2.43 (2.39–2.44) and maximum width 0.20 (0.19–0.22).

Lateral alae are present, triangular in cross section with a broad base and a pointed edge. Oral opening triangular, surrounded by one dorsal and two subventral lips. Except for two amphids, no cephalic sensory organs were visible. The oesophagus occupies the anterior third of the body and its total length is 0.81 (0.75–0.81). The isthmus is 0.65 (0.61–0.65) long and the bulbus round, 0.12 (0.11–0.12) long and 0.11 (0.09–0.12) wide. The nerve ring is 0.14 (0.14–0.16) from the anterior end and the excretory pore 1.04 (1.03– 1.10), approximately at mid-body.

The genital cone is prominent. The tip of the anterior anal lip is divided into two parts of variable shape (Fig. 1F and F’). The spicule is prominent and rather well-sclerotized, sharply pointed at both ends, 0.14 (0.13–0.15) long and 0.009 wide. A gubernaculum was not observed. The tail is 0.05 (0.04–0.06) long, stout and bent slightly ventrally, tapering to a pointed tip from the posterior half caudally.

TYPE LOCALITY

Klaserie Private Game Reserve (24°05’49.9”S; 31° 07’16.2”E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male and nine paratype males are deposited in the collection of the Museum National d’Histoire Naturelle, Paris, France, access number 283HS.

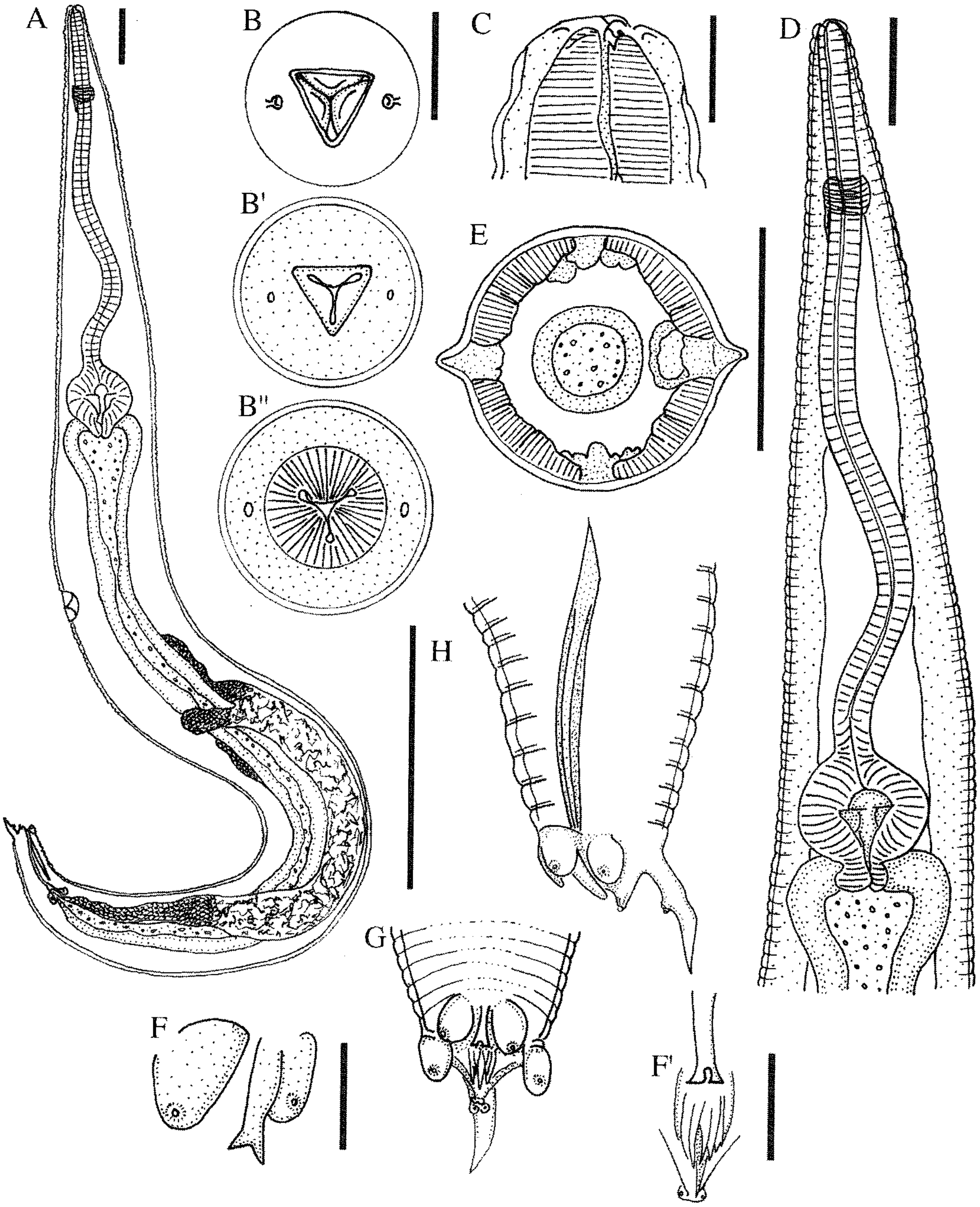

FIG. 1 *Thelandros schusteri*, male

- A Lateral view of the entire nematode
- B Apical view of the head
- B' Transverse section through the anterior part, 0.002 mm and 0.023 mm below the apex respectively
- C Median view of the head
- D Lateral view of the anterior region
- E Transverse section at mid-body showing the lateral alae and the shape of the body
- F Variations in the anterior anal lip with the genital cone, subventral view
- F' Variations in the anterior genital papillae, ventral view
- G Ventral view of the posterior end
- H Lateral view of the posterior end, showing the position of the spicule

Scale bars: A, D, E, G, H—0.1 mm; B, B', B'', C, F F'—0.02 mm

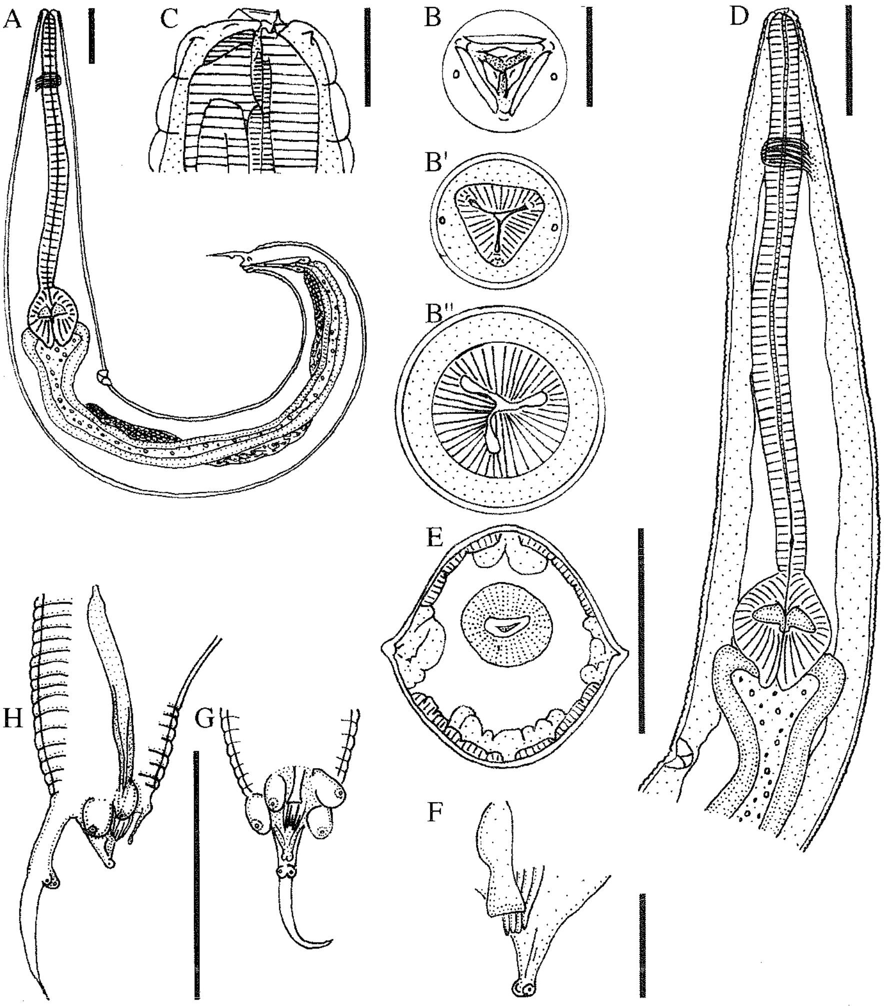

FIG. 2 *Thelandros boomkeri*, male

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B"	Transverse section through the anterior part, 0.004 mm and 0.018 mm below the apex respectively
C	Median view of the head
D	Lateral view of the anterior region
E	Transverse section at mid-body showing the lateral alae and the shape of the body
F	Detail of the anterior anal lip with the genital cone, subventral view
G	Ventral view of the posterior end
H	Lateral view of the posterior end, showing the position of the spicule

Scale bars: A, D, E, G, H—0.1 mm; B, B' B", C, F—0.02 mm

HABITAT

Stomach and large intestine.

Thelandros boomkeri **Hering-Hagenbeck, 2001**
(Fig. 2)

MALE (*n* = 3)

The worms are 1.89 (1.75–1.90) in length and 0.15 (0.14–0.18) in maximum width. Lateral alae are present, pointed in cross-section. The oral opening is triangular, surrounded by one dorsal and two subventral lips. Just below the lips, three triangular tooth-like projections are present. Except for amphids, no cephalic papillae were observed. The oesophagus is 0.69 (0.62–0.70) long, the isthmus 0.57 (0.53–0.59), and the round bulbus is 0.09 (0.08–0.11) long and 0.10 (0.09–0.12) wide. The nerve ring is 0.15 (0.14–0.16) from the anterior end and the excretory pore 0.85 (0.72–0.85), just posterior to the oesophago-intestinal junction.

The anterior anal lip is plain, with rounded or pointed edges (Fig. 2F). The spicule is slightly arcuate, its distal extremity curved ventrally, its total length 0.13 (0.11–0.13) and the maximum width 0.009. A gubernaculum is absent. The caudal extremity is 0.08 (0.07–0.09) long, slender and often curved ventrally.

TYPE LOCALITY

Hoedspruit Air Base Nature Reserve (24°19'18"S; 31°01'39.2"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male and two paratype males are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 284HS.

HABITAT

Stomach and large intestine.

Thelandros luciusi **Hering-Hagenbeck, 2001**

(Fig. 3)

MALE (*n* = 3)

Total length 2.52 (1.99–2.65) with a maximum width of 0.19 (0.16–0.22) at mid-body. Lateral alae are absent. The oral opening is triangular and surrounded by one dorsal and two subventral, sharply pointed, cuticular lips. Except for the amphids, cephalic sense organs are not visible. The lumen of the oesophagus is twisted (Fig. 3B" and B"') and its total length is 0.77 (0.71–0.82). The isthmus is 0.60 (0.57–0.65) from the anterior end and the bulbus is round, 0.09 (0.09–0.12) long and 0.11 (0.10–0.12) wide. The nerve ring is 0.13 (0.13–0.18) from the anterior end and the excretory pore 1.06 (0.86–1.12), always posterior to the bulbus.

The tip of the anterior anal lip is divided into between five to more than ten branches (Fig. 3F and F'). The spicule is prominent and well sclerotized, more or less straight, 0.13 (0.13–0.15) long and 0.014 (0.012–0.014) wide. Gubernaculum not seen. The tail is 0.13 (0.12–0.15) long and slender, strongly curved ventrally.

TYPE LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male and two paratype males are deposited in the collections of the Museum National d'Histoire Naturelle, Paris, France, access number 285HS.

HABITAT

Stomach and large intestine.

Discussion

According to Adamson (1981) and Adamson & Nasher (1984), *Thelandros* is readily distinguishable from *Parapharyngodon*, to which it is closely related, by the presence of a prominent genital cone, a marked distance between the anus and the spicule pouch, and the caudal pre- and adanal papillae which are pedunculated in *Thelandros* but mammilliform in *Parapharyngodon*. The eggs of *Thelandros* have terminal opercula and *in utero* already contain a larva. In addition, the genus *Parapharyngodon* occurs in insectivorous reptiles.

Members of the genus *Thelandros* occur in herbivorous and omnivorous hosts (Adamson 1981), predominantly in *Agama* spp. and *Uromastix* spp. (Agamidae). The omnivorous Gerrhosauridae have never before been described as suitable hosts for *Thelandros*. Of the more than 15 described species, the three redescribed here most closely resemble *Thelandros chabaudi* Caballero, 1968 from *Oplurus quadrimaculatus* in Madagascar, *Thelandros agama* Adamson & Nasher, 1984 from *Agama yemenensis* from Saudi Arabia and *Thelandros alatus* from *Uromastix* spp. in Egypt, Tunisia, Algeria and Afghanistan (Barûs & Tenora 1976) especially in the general structure of the caudal extremity. However, *Thelandros chabaudi, Thelandros agama* and *Thelandros alatus* all have spicules shorter than 0.1 mm. Furthermore, *Thelandros agama* has caudal alae, which are lacking in the three redescribed species. The tail of *Thelandros chabaudi* appears more solid and the last pair of papillae, situated in the posterior half of the tail, seem much smaller than is the case with the species redescribed here.

In South Africa the genus *Thelandros* is represented by four species parasitic in tortoises. The fifth species, *Thelandros sexlabiata* Ortlepp, 1933, has been removed from the genus by Adamson & Nasher (1984).

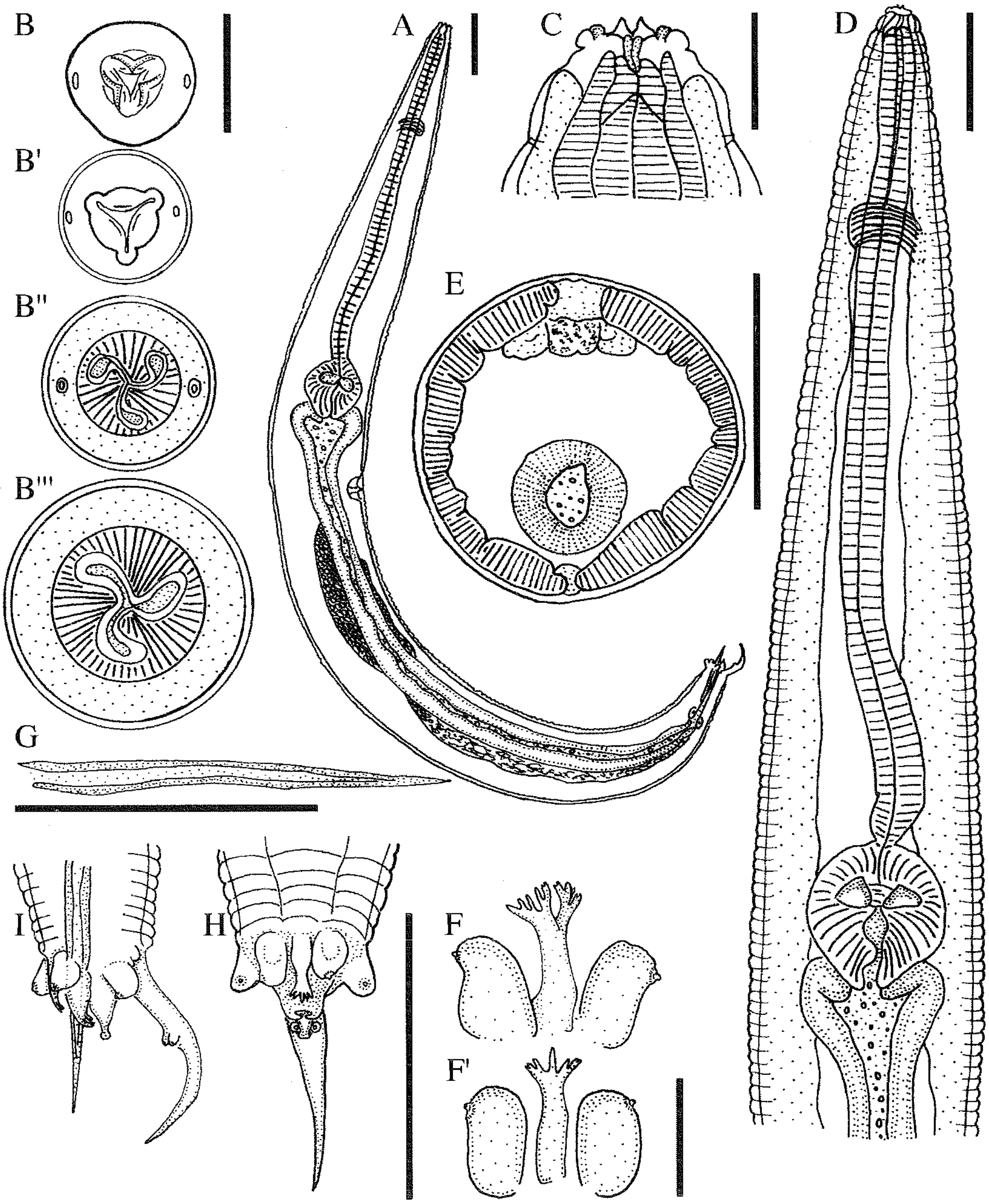

FIG. 3 *Thelandros luciusi*, male

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B'''	Transverse section through the anterior part, 0.002 mm, 0.012 mm and 0.023 mm below the apex respectively
C	Median view of the head
D	Lateral view of the anterior region
E	Transverse section at mid-body showing the shape of the body
F	Variations of the anterior anal lip with the anterior genital papillae, ventral view
G	Lateral view of the spicule
H	Ventral view of the posterior end
I	Lateral view of the posterior end, showing the position of the spicule

Scale bars: A, D, E, G, H, I—0.1 mm; B, B', B'', B''', C, F, F'—0.02 mm

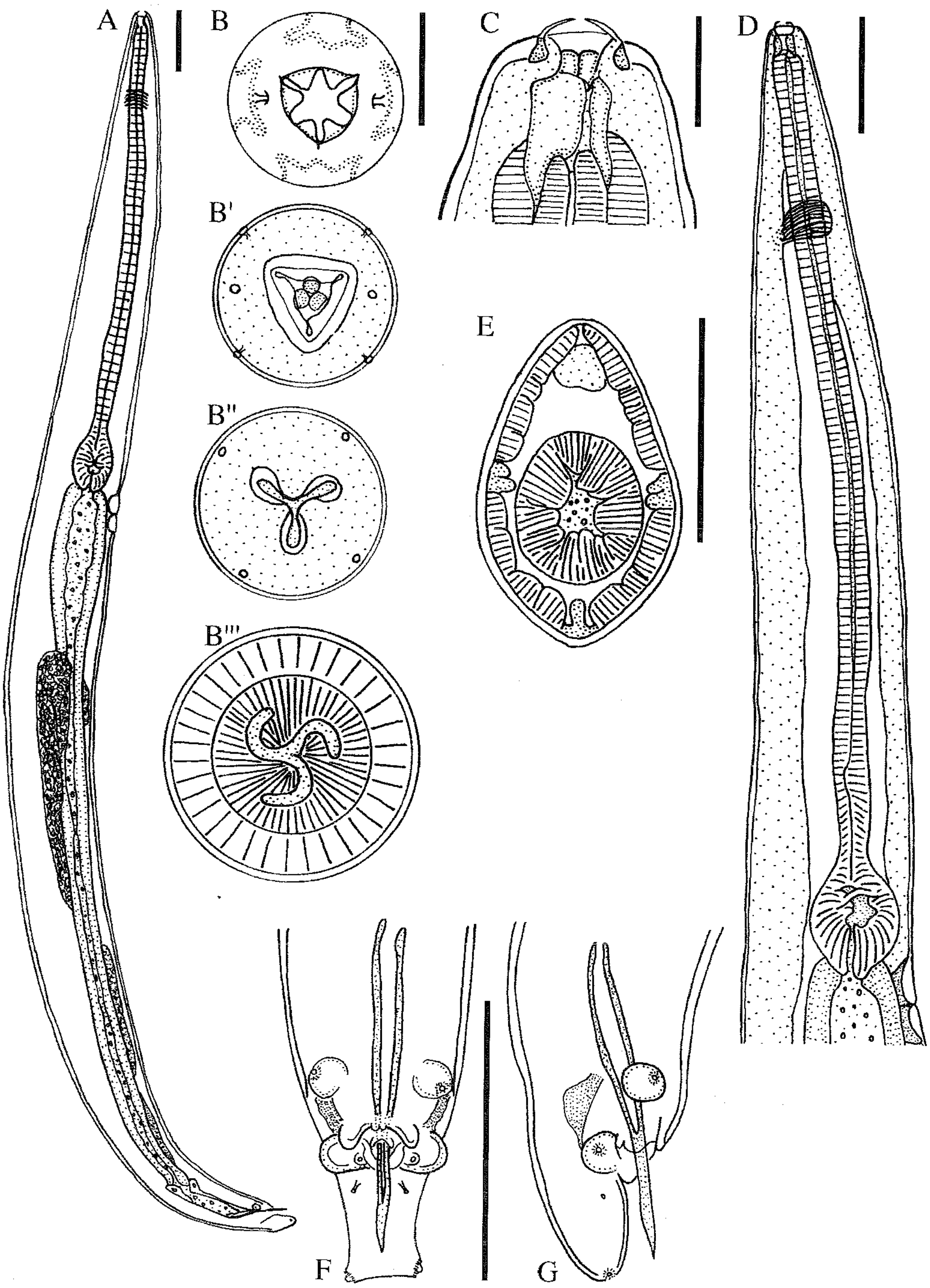

FIG. 4 *Tachygonetria bainae*, male

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B'''	Transverse sections of the anterior part, 0.004, 0.008 and 0.02 mm from the apex respectively
C	Median view of the head
D	Lateral view of the anterior region
E	Transverse section at mid-body, showing the body shape
F	Ventral view of the posterior end
G	Lateral view of the posterior end

Scale bars: A, D, E, F, G—0.1 mm; B, B', B'', B'''—0.02 mm

Thelandros ortleppi Petter, 1966 differs from the redescribed species in having large caudal alae. Petter (1966) considered *Thelandros versterae* Petter, 1966, *Thelandros weilliae* (Petter, 1966) and *Thelandros tcheprakovae* (Petter, 1966) to be three subspecies of *Thelandros versterae*. They are close to the redescribed species but the caudal papillae are bigger and more distant from one another. In addition, the spicules of *Thelandros versterae*, *Thelandros weilliae* and *Thelandros tcheprakovae* are shorter than those of the species redescribed, and the oesophagi of *Thelandros versterae* and *Thelandros weilliae* are very short. The characteristic shape of the anterior anal lip differs distinctly between *Thelandros schusteri*, *Thelandros boomkeri* and *Thelandros luciusi* and their shape is also unique among the existing species. The configuration of this delicate appendage should be taken into consideration in future studies.

CHARACTERIZATION OF THE GENUS *TACHYGONETRIA* WEDL, 1862

TYPE SPECIES: *Tachygonetria vivipara* Wedl, 1862

Pharyngodonidae. Body cuticle with distinct transverse striations. Caudal extremity of the male abruptly truncate posterior to the last pair of caudal papillae and often supported by a short caudal spine. The last pair of caudal papillae is situated almost laterally. Widely distributed parasites of herbivorous and omnivorous reptiles, mainly tortoises (Petter 1966; Adamson & Nasher 1984).

Redescription of the species *Tachygonetria bainae* Hering-Hagenbeck, 2001 (Fig. 4)

MALE (*n* = 20)

Body 2.64 (2.44–2.64) long and 0.22 (0.18–0.22) wide near the mid-body. In cross-section the body is ovoid with the narrower part dorsally, and without lateral alae. The cephalic extremity is flattened and the apex ornamented with four cuticular relief patterns (Fig. 4B), the two lateral ones of which enclose an amphid. Amphids have two projections. Four cephalic papillae, visible 0.004 below the apex, occur on the edges of the ventral and dorsal relief patterns. The mouth opening is triangular, guarded by two dorsal, two lateral and two ventral membranous cuticular flaps. The cuticular lining at the anterior end of the oesophagus forms two lateral and one dorsal, anteriorly directed, tooth-like structures. The oesophagus is 0.87 (0.84–0.91) long, with a twisted inner margin (Fig. 4B'''). The isthmus is 0.74 (0.71–0.78) from the anterior end and the bulbus is subspherical, 0.09 (0.09–0.10) long and 0.11 (0.09–0.11) wide. The nerve ring is 0.20 (0.18–0.21) from the anterior end and the excretory pore 1.02 (0.91–1.04), always posterior to the oesophago-intestinal junction.

The anterior anal lip is formed by two prominent fleshy lobes, enclosing two small projections, while the posterior anal lip is supported by a hardly visible accessory piece. Four pairs of caudal papillae are present (Fig. 4F): one pre-anal and subventral pair of large pedunculated rosette papillae, a second pair has the same shape and size but lie adanal, the third pair is small and sessile, and occurs more median while the fourth and most posterior pair is visible on the lateral end of the caudal appendage. The caudal alae, 0.027 long and 0.009 wide, are present between the first and the second pairs of papillae. The well-sclerotized and prominent spicule is 0.12 (0.12–0.14) long and 0.011 wide. The tail is 0.06 (0.05–0.06) long.

TYPE LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male and 19 paratype males are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 286HS.

HABITAT

Stomach and large intestine.

Tachygonetria petterae Hering-Hagenbeck, 2001 (Fig. 5)

MALE (*n* = 3)

Body 2.11 (2.08–2.11) long and 0.13 (0.09–0.13) wide near the mid-body. Minute lateral alae are present, and the body is almost square in cross section. The cephalic extremity is flattened and the mouth opening triangular, without lips. The cephalic sense organs consist of four dorsal and four subventral papillae. Amphids occur between the outer subventral and dorsal cephalic papillae (Fig. 5B). The oesophagus measures 0.50 (0.47–0.50), the isthmus 0.37 (0.36–0.38) and the bulbus is more or less round, 0.09 (0.06–0.09) long and 0.09 (0.08–0.09) wide. The nerve ring is in the anterior fourth

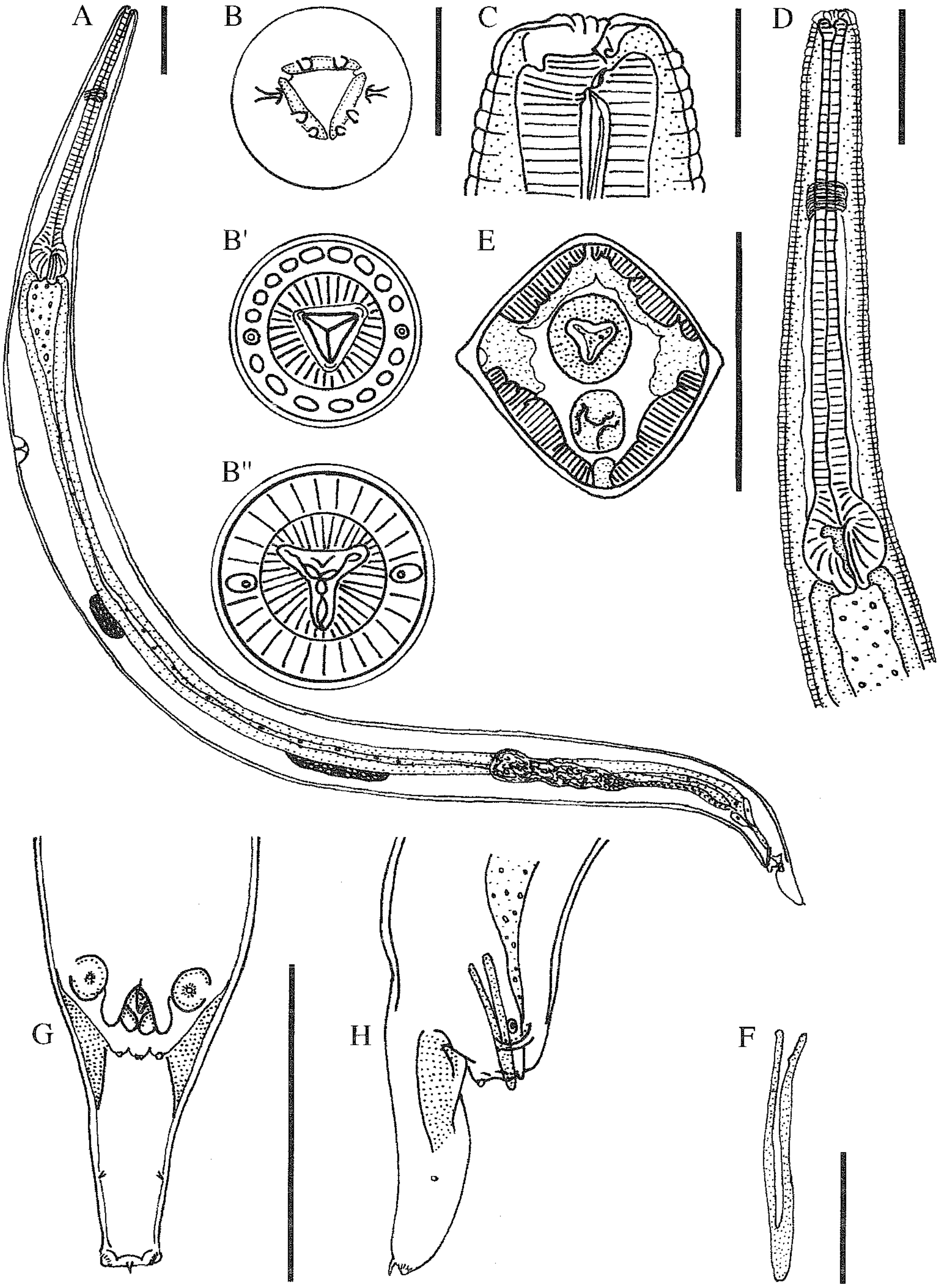

FIG. 5 *Tachygonetria petterae*, male

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B"	Transverse sections of the anterior part, 0.007 and 0.014 mm from the apex respectively
C	Median view of the head
D	Lateral view of the anterior region
E	Transverse section at mid-body, showing the body shape
F	Lateral view of the spicule
G	Ventral view of the posterior end
H	Lateral view of the posterior end

Scale bars: A, D, E, G, H—0.1 mm; B, B', B", C, F—0.02 mm of the oesophagus, 0.15 (0.10–0.12) from the apex and the excretory pore 0.70 (0.69–0.71), always posterior to the bulbus.

The anterior anal lip is formed by two long, fleshy, curved lobes connected by a membranous cuticular sheath. Four pairs of caudal papillae are present (Fig. 5G), a subventral, mammilliform pre-anal pair, a smaller, adanal pedunculated second pair, covered by the anterior anal lip and a third pair, median and postanal, similar in size and shape as the first pair. Two tiny projections are present on the tip of the posterior anal lip. The fourth pair of papillae occurs laterally on the posterior end of the caudal appendage. The latter is 0.045 (0.040–0.049) long and bears a minute terminal spine. Caudal alae, 0.022 long and 0.011 wide, are present on the anterior half of the caudal extremity. The spicule is weakly sclerotized, 0.051 long and 0.004 wide, with a rounded distal end.

TYPE LOCALITY

Timbavati Private Game Reserve (24°0.5'51.4"S; 31°0.7'18.1"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male and two paratype males are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 287HS.

HABITAT

Stomach and large intestine.

Tachygonetria chabaudi **Hering-Hagenbeck, 2001** (Fig. 6)

MALE (*n* = 20)

Males are 1.75 (1.72–1.81) long with a maximum width of 0.11 (0.09–0.12). Lateral alae are not visible. The body outline is almost square in cross-section. The anterior extremity is flattened and the triangular mouth opening is without lips. Cephalic sense organs consist of four dorsal and four subventral papillae. Amphids are present between the outer subventral and dorsal cephalic papillae (Fig. 6B). The oesophagus is 0.44 (0.41–0.45) long, the isthmus 0.34 (0.30–0.34) and the bulbus is slightly oval, 0.07 (0.06–0.07) long and 0.06 (0.06–0.07) wide. The nerve ring is 0.11 (0.10–0.12) from the apex, at the end of anterior third of the oesophagus, and the excretory pore is always posterior to the bulbus, 0.59 (0.57–0.63) from the apex.

Four pairs of caudal papillae are present (Fig. 6E); a prominent pre-anal pair, mammilliform and situated subventrally, a second adanal pair is long and pedunculated and enclosed by the anterior anal lip. The latter is formed by two half-moon-shaped cuticular flaps. Pair three occurs median and postanal and is similar in size and shape to the first pair. Between pair 3 a single, minute papillae-like projection is present. The fourth pair occurs laterally on the posterior end of the caudal appendage. The latter is 0.06 (0.05–0.07) long, and carries a minute terminal spine. Caudal alae, 0.040 long and 0.016 wide, are present in the anterior half of the caudal extremity. The spicule is straight, with a rounded distal extremity, and is 0.037 (0.036–0.043) long and 0.005 wide.

TYPE LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

The holotype male and 19 paratype males are deposited in the collections of the Museum National d'Histoire Naturelle, Paris, France, access number 288HS.

HABITAT

Stomach and large intestine.

Discussion

Tachygonetria, as one of the nine pharyngodonid genera which occur in herbivorous and omnivorous reptiles (Petter & Douglass 1976; Petter & Quentin 1976), is one of the most widely distributed. Together with the genera *Alaeuris* Thapar, 1925 and *Thaparia* Ortlepp, 1933 it is found in the Ethiopian, Oriental, Madagascan, Neotropical, Palaearctic and Nearctic regions. Their absence from the Australian continent is probably the result of the absence of terrestrial tortoises (Adamson & Nasher 1984). *Tachygonetria* is essentially a parasite of tortoises, particularly of the genus *Testudo* (Petter 1966).

Currently more than 20 *Tachygonetria* species are known. Except for the type species *Tachygonetria vivipara* Wedl, 1862, a parasite of *Uromastix* spp. (Agamidae) in Egypt, Morocco and Algeria (Baylis

1923; Baker 1987) and *Tachygonetria paradentata* Adamson & Nasher, 1984 from *Agama yemenensis* in Saudi Arabia, all the other species are known from chelonians.

Because of the presence of characteristically broad cephalic extremities, *Tachygonetria chabaudi* and *Tachygonetria petterae* belong to the "*Tachygonetria dentata*" complex, which currently includes the five species *Tachygonetria dentata* Drasche, 1883, *Tachygonetria paradentata*, *Tachygonetria quentini* Petter, 1966, *Tachygonetria richardae* Petter, 1966 and *Tachygonetria nearctica* Petter & Douglass, 1976. The last named three species were originally described as subspecies of *Tachygonetria dentata* by Petter (1966) and Petter & Douglass (1976). The species *Tachygonetria quentini* is parasitic in tortoises in South Africa and, although closely related, differs from the species redescribed here by the absence of caudal alae. With the exception of *Tachygonetria paradentata*, none of the species mentioned above has alae at the base of the caudal appendage. *Tachygonetria chabaudi* and *Tachy-*

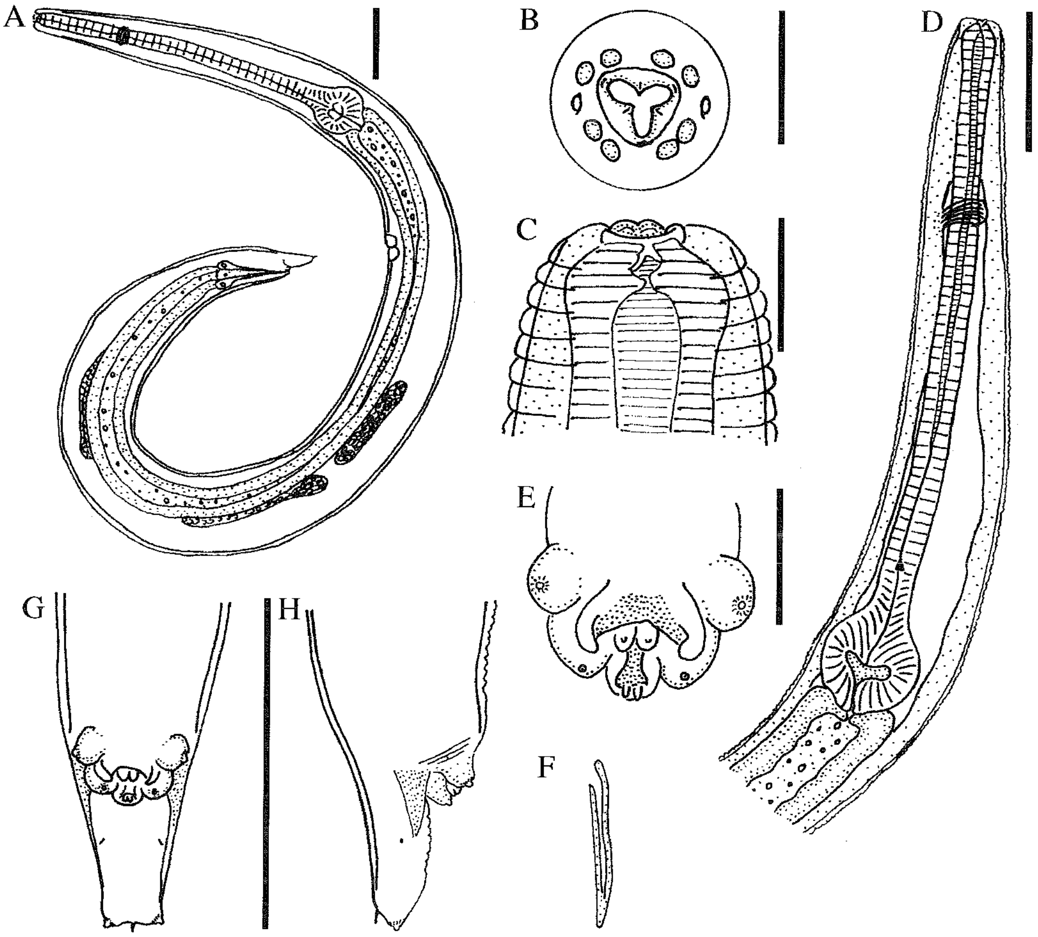

FIG. 6 *Tachygonetria chabaudi*, male

A	Lateral view of the entire nematode
B	Apical view of the head
C	Median view of the head
D	Lateral view of the anterior region
E	Ventral view of the genital cone and associated papillae
F	Lateral view of the spicule
G	Ventral view of the posterior end
H	Lateral view of the posterior end

Scale bars: A, D, F, G, H— 0.1 mm; B, C, E—0.02 mm *gonetria petterae* both lack tooth-like structures in the buccal cavity, which are present in *Tachygonetria paradentata*, and both have slightly longer tails. Furthermore, they differ by the appearance of the anterior and posterior anal lips which appear more elongated and thicker in the last-named species.

In its general appearance, *Tachygonetria bainae* resembles *Tachygonetria longicollis fitzsimonsi* Petter, 1966 from *Geochelone pardalis* in Swaziland and the Pretoria zoo. This subspecies also has six cuticular flaps in the mouth opening, lacks a terminal spine, has a prominent spicule which is slightly longer than the tail and a conspicuously long oesophagus. The tail of *Tachygonetria bainae* is more robust and shorter than that of *Tachygonetria l. fitzsimonsi,* the spicule is slightly longer and different in shape, the phasmids are located more anteriorly and *Tachygonetria l. fitzsimonsi* lacks caudal alae.

The genus *Tachygonetria* is highly host-specific and our three species are the first to be recorded from the family Gerrhosauridae.

***Thelandros* and *Tachygonetria* females**

FEMALE TYPE A (*n* = 20) (Fig. 7)

Round nematodes, tapering towards both extremities and without lateral alae. Total length 4.87 (4.55–5.01) and maximum width 0.36 (0.36–0.45) near mid-body. Cephalic extremity flattened. Mouth opening triangular, surrounded by one dorsal and two broad subventral membranous cuticular flaps. Cephalic papillae consisting of four submedian pairs of nerve endings and two amphids. Nerve endings are surrounded by prominent U-shaped cuticular relief patterns. Below the apex, at the anterior end of the oesophagus, the cuticular lining forms one dorsal and two subventral serrated, tooth-like structures.

The oesophagus is 0.61 (0.53–0.65) long and of more or less uniform width, the isthmus is distinct, 0.45 long, and a bulbus, 0.12 (0.11–0.31) long and 0.12 (0.10–0.29) wide, is present. At the oesophago-intestinal junction the intestine is clavate, and is as wide as the body. The conspicuous nerve ring is 0.17 (0.17–0.19) from the anterior end, the excretory pore 1.26 (1.19–1.30) and the vulva 2.33 (2.25–2.42), more or less at mid-body.

The prominent muscular vagina is directed anteriorly but flexes posteriorly into a common uterus. The latter divides near the anus and the uteri run anteriorly, reaching the oviducts near the level of the vulva. The blind ends of the ovaries extend to just anterior of the excretory pore. Eggs measure 0.127 x 0.073, are thin-shelled, with a small polar operculum and are not embryonated when laid. The tail is 0.42 (0.37–0.43) long.

HOST LOCALITY

Timbavati Private Game Reserve (24°24’56.5”S; 31°17’50.8”E), Northern Province, Republic of South Africa.

TYPE MATERIAL

Twenty females are deposited in the collection of the Museum National d’Histoire Naturelle, Paris, France, access number 289HS.

HABITAT

Stomach and large intestine.

FEMALE TYPE B (*n* = 20) (Fig. 8)

Body 3.53 (3.36–3.69) long and 0.27 (0.22–0.30) wide near mid-body; lateral alae are absent. The triangular mouth opening is covered by one dorsal and two broad subventral membranous cuticular flaps. The distal margins of the latter enclose two conspicuous papillae dorsally, and the subventral ones a prominent amphid and a distinct papilla each. The buccal capsule is markedly thickened dorsally and subventrally, and one dorsal and two subventral projections, subtriangular in apical view, arise from the anterior end of the oesophagus.

The oesophagus is 0.52 (0.49–0.53) long, and the maximum width is attained immediately behind the buccal capsule. The distinct isthmus is 0.31 (0.30–0.31) from the anterior end and the bulbus is oval, slightly longer than wide, measuring 0.13 (0.10–0.13) x 0.11 (0.09–0.12). The nerve ring lies 0.14 (0.12–0.14) from the apex, and the excretory pore 1.18 (1.16–1.22), both in the anterior third of the body.

The vulva lies just anterior to the anus, 2.96 (2.84–3.13) from the anterior end. Its opening is directed posteriorly and a prominent pre-vulvar swelling, almost forming a flap over the vulva, is present. The short muscular vagina with a conspicuous sphincter runs anteriorly, joins the common uterus which turns posteriorly and divides into two uteri at the level of the vulva. The uteri then turn anteriorly, going over into the oviducts. The ovaries coil around the intestine and their blind ends terminate just posterior to the oesophago-intestinal junction, often facing posteriorly. Eggs measure 0.113 x 0.054, are thin-shelled and operculated, and contain a morula when laid. The tail is 0.26 (0.26–0.29) long, tapering strongly immediately behind the anus to end in a blunt tip.

HOST LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

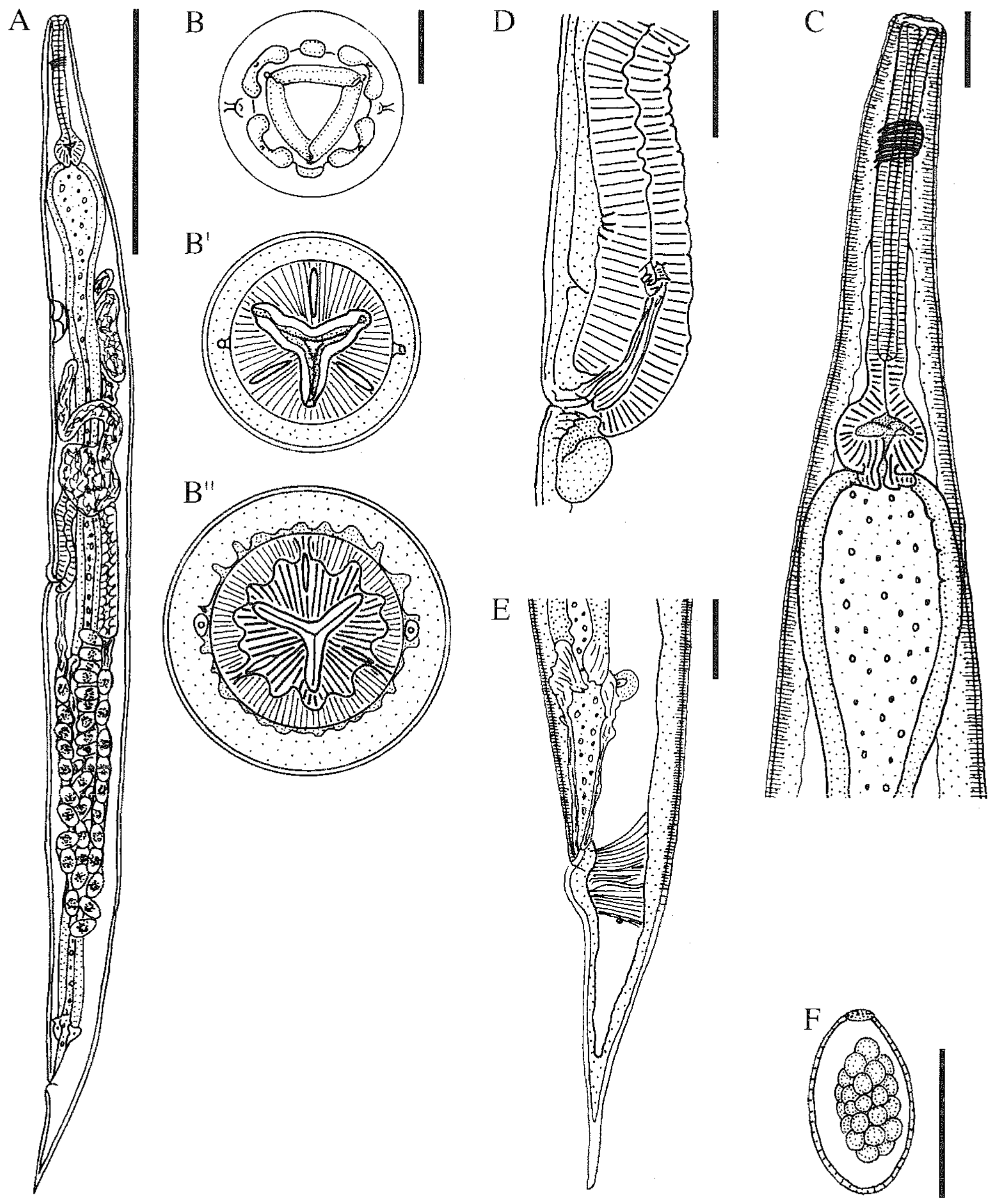

FIG. 7 Female type A

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B"	Transverse sections of the anterior part, 0.008 and 0.024 mm from the apex respectively
C	Lateral view of the anterior region
D	Lateral view of the vulva and ovejector
E	Lateral view of the posterior end
F	Egg

Scale bars: A—1 mm; C, D, E, F—0.1 mm; B, B', B"—0.02 mm

TYPE MATERIAL

Twenty females, deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 290HS.

HABITAT

Stomach and large intestine.

FEMALE TYPE C (*n* = 20) (Fig. 9)

The nematodes are spindle-shaped and the body is subhexagonal in transverse section. They are 4.64 (4.36–4.74) long and 0.47 (0.45–0.51) wide at mid-body. Lateral alae are absent. The cephalic extremity is slightly flattened. Lips are absent and the subtriangular mouth opening is guarded by one dorsal and two broad subventral membranous cuticular flaps. Just below the flaps, the cuticular lining forms one dorsal and two subventral serrated tooth-like structures. Cephalic sense organs consist of four pairs of submedian papillae, at the sides of the apex, and two lateral amphids. Below the apex, at the anterior end of the oesophagus, are three tooth-like structures.

The oesophagus is extremely long, 1.58 (1.54–1.69), and its inner margin is slightly twisted. The isthmus is 1.39 from the anterior end, and the bulbus is small and round, 0.13 (0.13–0.15) x 0.13 (0.13–0.16) in diameter. The intestine at the oesophago-intestinal junction is club-shaped with a maxi-

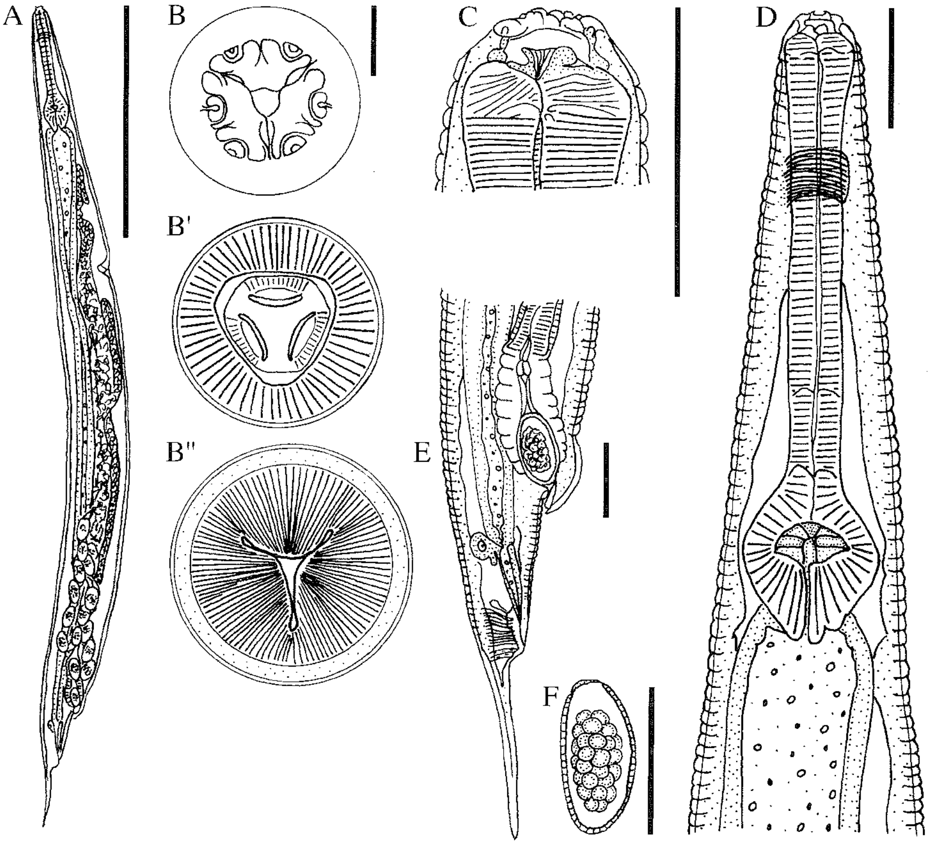

FIG. 8 Female type B

A Lateral view of the entire nematode
B Apical view of the head
B'–B" Transverse sections of the anterior part, 0.011 and 0.024 mm from the apex respectively
C Median view of the head
D Lateral view of the anterior region
E Lateral view of the posterior end
F Egg

Scale bars: A—1 mm; C, D, E, F—0.1 mm; B, B', B"—0.02 mm

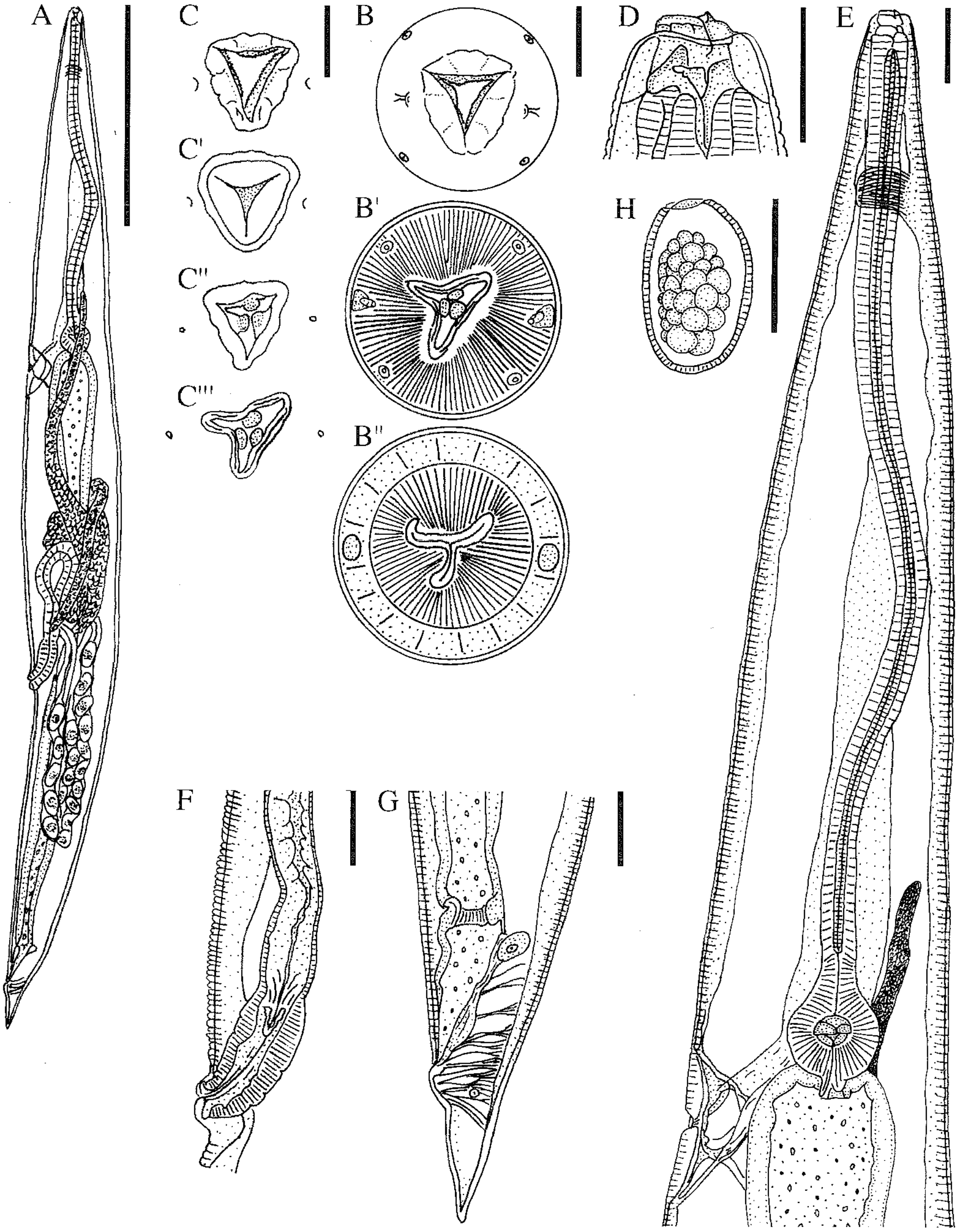

FIG. 9 Female type C

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B"	Transverse sections of the anterior part, 0.016 and 0.037 mm from the apex respectively
C	Apical view
C'–C'"	Transverse sections of the pharynx, 0.006, 0.01 and 0.016 mm from the apex respectively. Note the tooth-like structures in C" and C'"
D	Median view of the head
E	Lateral view of the anterior region
F	Lateral view of the vulvar region
G	Lateral view of the posterior end
H	Egg

Scale bars: A—1 mm; D, E, F, G, H—0.1 mm; B, B', B",C, C', C" C'"—0.02 mm mum width exceeding that of the bulbus by 1.5 times. The nerve ring is 0.27 (0.26–0.58) from the anterior end and the conspicuous excretory pore 1.62 (1.60–1.83), just posterior to the bulbus.

The vulva lies in the posterior body half 3.02 (2.84–3.18) from the apex. The short muscular vagina runs anteriorly, joins a common uterus which turns posteriorly and divides halfway between the vulva and the anus into two anteriorly directed uteri. The uteri become the oviducts at about the level of the vulva. The ovaries extend anteriorly for a short distance, the one turning posteriorly and ending anterior to the ovejector, the other extending anteriorly to beyond the level of the bulbus. Eggs are large, thin-shelled, with prominent polar opercula and unsegmented when laid. They measure 0.132 x 0.081. The tail is 0.19 (0.16–0.19) long.

HOST LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

Twenty females are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 291HS.

HABITAT

Stomach and large intestine.

FEMALE TYPE D (*n* = 20) (Fig. 10)

The total length is 4.64 (4.36–4.74) and the maximum width 0.47 (0.45–0.51) near mid-body; lateral alae absent. The triangular mouth opening is covered by six rounded lips, the two subventral and two dorsal ones ornamented and each bearing a single cephalic papilla, the two lateral lips plain and bearing amphids. Just below the lips, at the anterior end of the oesophagus, the prominent cuticular lining forms one dorsal and two subventral, serrated, tooth-like structures.

The oesophagus is 0.77 (0.76–0.84) long and the isthmus is 0.55 from anterior end. The bulbus is round, 0.17 (0.16–0.18) long and 0.17 (0.16–0.18) wide. The intestine envelops the posterior third of the bulbus. The nerve ring is 0.14 (0.13–0.16) from the apex. A prominent excretory pore is present in the anterior third of the body, 1.36 (1.33–1.41) from the anterior end and the vulva 2.93 (2.84–3.10), at the start of the posterior third of the body. The vulva opening is directed posteriorly. A short muscular vagina with a conspicuous sphincter runs anteriorly, joins a common uterus which turns posteriorly and divides into two just posterior to the vulva. The two uteri run anteriorly going over into the oviducts. The ovaries coil around the intestine, one blind end turning posteriorly and the other anteriorly, the latter reaching the level of the excretory pore. Eggs measure 0.104 x 0.056, are thin shelled and operculated and laid in the morula stage. The tail measures 0.48 (0.29–0.52) and tapers strongly immediately behind the anus to end in a blunt tip.

HOST LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

Twenty females are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 292HS.

HABITAT

Stomach and large intestine.

FEMALE TYPE E (*n* = 20) (Fig. 11)

The body is 4.04 (3.88–4.15) long and 0.29 (0.28–0.38) wide at mid-body. The cephalic extremity is slightly flattened and lips are absent. The triangular mouth opening is surrounded by six bean-shaped cuticular elevations. Except for amphids no cephalic sense organs were observed. Below the apex, at the anterior end of the oesophagus, three prominent tooth-like structures are present.

The long oesophagus measures 1.06 (1.02–1.14). The indistinct isthmus is 0.91 (0.88–0.96) from the anterior end and the small, oval bulbus is 0.12 (0.12–0.15) long and 0.14 (0.14–0.17) wide. The intestine has approximately the same width as the bulbus and envelops the latter. The nerve ring is 0.19 (0.17–0.19) from the apex, the excretory pore 1.47 (1.47–1.60), in the anterior half of the body, and the vulva 2.87 (2.76–2.96) from the anterior end, in the posterior third of the body.

Prominent post-vulvar and less prominent pre-vulvar swellings are present. The short muscular vagina runs anteriorly into a common uterus, which turns posteriorly and divides into two, halfway between the vulva and the anus. The uteri run anterior and go over into the oviducts near the middle of

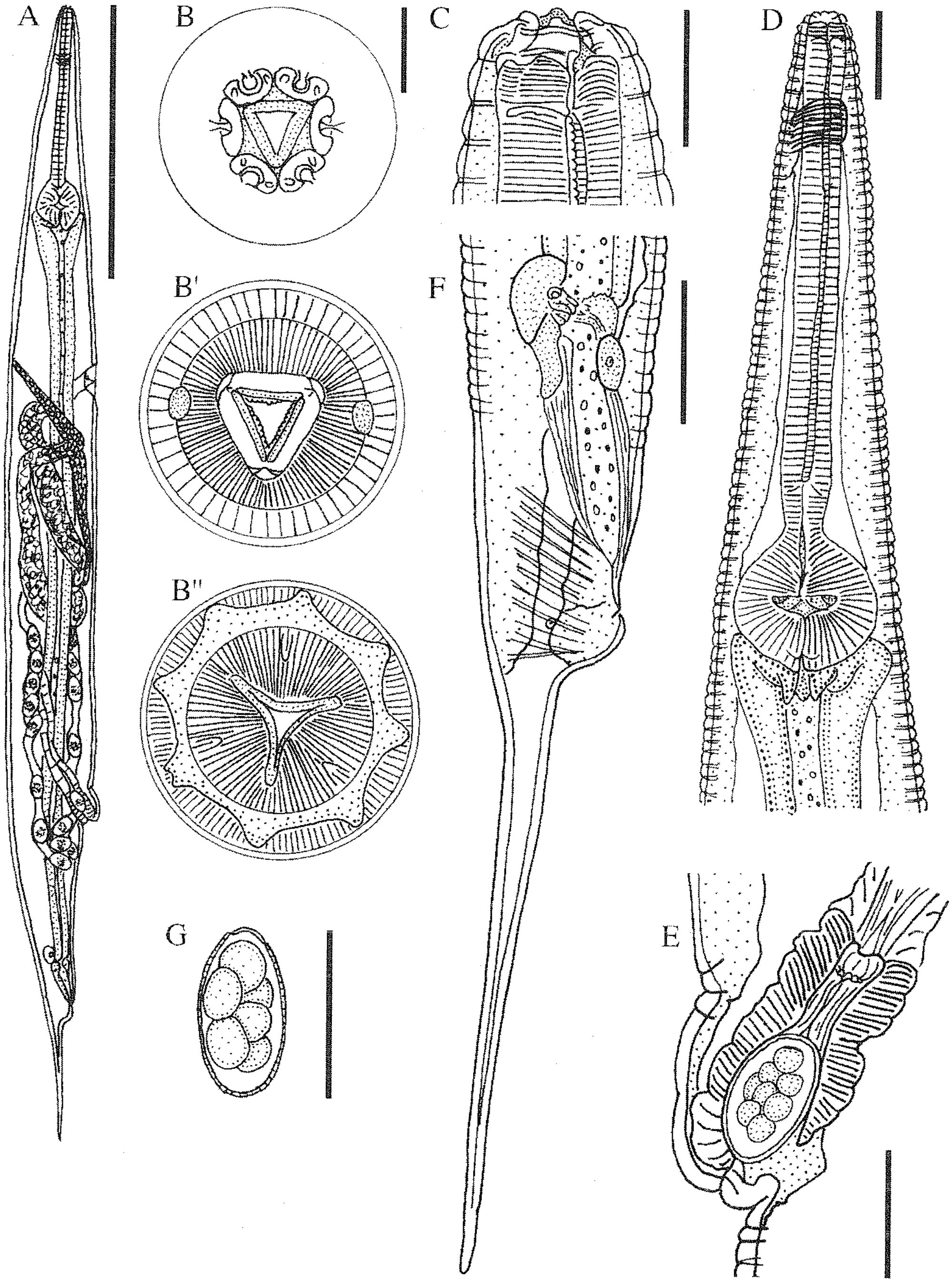

FIG. 10 Female type D

A Lateral view of the entire nematode
B Apical view of the head
B'–B'' Transverse sections of the anterior part, 0.011 and 0.024 mm from the apex respectively
C Median view of the head
D Lateral view of the anterior region
E Lateral view of the vulvar region. An egg is present in the ovejector
F Lateral view of the posterior end
G Egg

Scale bars: A—1 mm; D, E, F, G—0.1 mm; C—0.05 mm; B, B', B''—0.02 mm

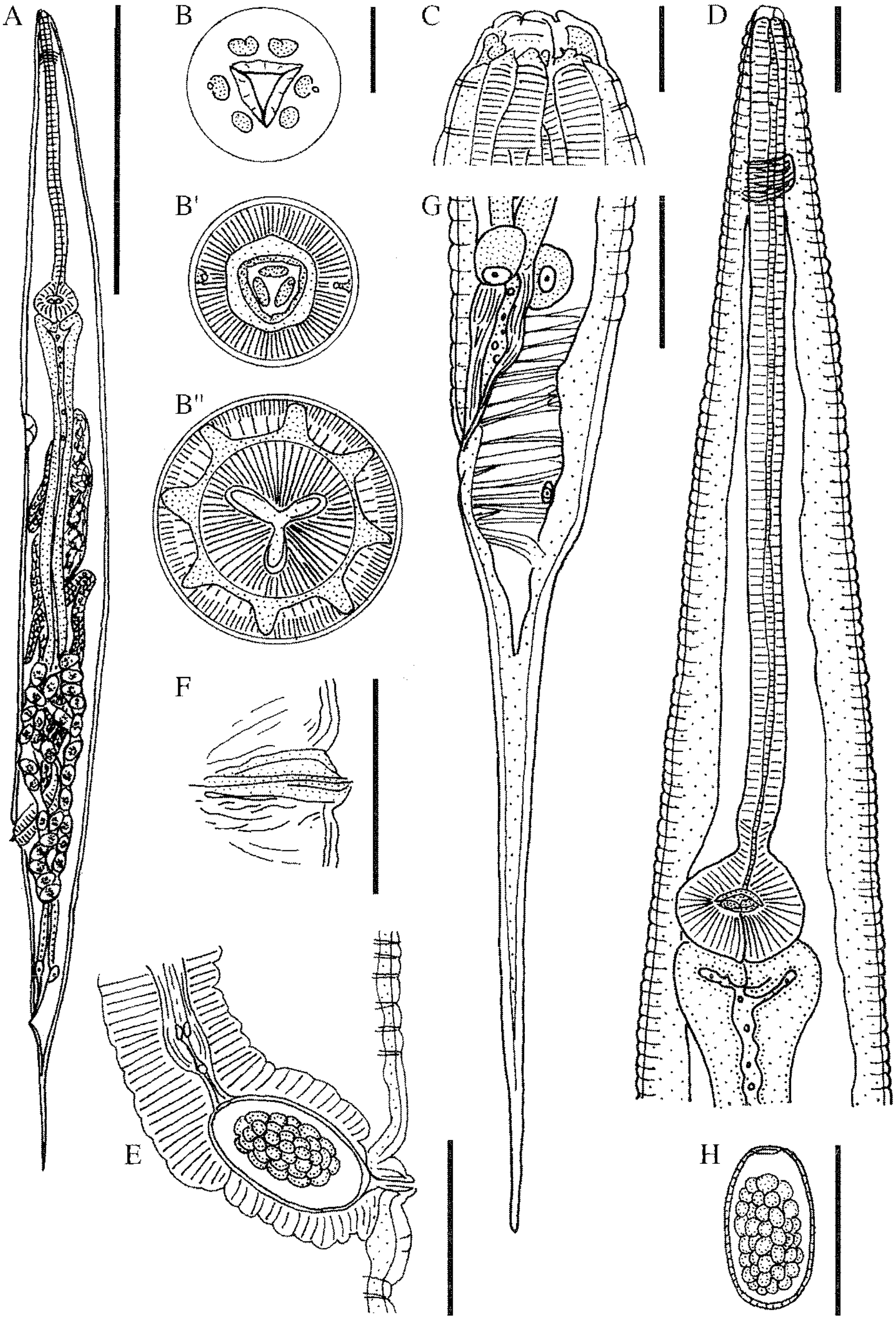

FIG. 11 Female type E

A	Lateral view of the entire nematode
B	Apical view of the head
B'–B"	Transverse sections of the anterior part, 0.012 and 0.034 mm from the apex respectively
C	Median view of the head
D	Lateral view of the anterior region
E	Lateral view of the vulvar region. An egg is present in the ovejector
F	Lateral view of the vulva
G	Lateral view of the posterior end
H	Egg

Scale bars: A—1 mm; D, E, F, G, H—0.1 mm; B, B', B", C—0.02 mm the body. The blind ends of the ovaries terminate near the excretory pore. Eggs measure 0.095 x 0.054, are thin- shelled, have a terminal operculum and are deposited in early stage of cleavage. The tail is thin and 0.52 (0.52–0.59) long.

HOST LOCALITY

Timbavati Private Game Reserve (24°24'56.5"S; 31°17'50.8"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

Twenty females are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 293HS.

HABITAT

Stomach and large intestine.

FEMALE (TYPE F) (*n* = 5) (Fig. 12)

Stout nematodes, dorsally curved when fixed, 4.38 (2.86–4.38) long and 0.51 (0.25–0.51) wide at mid-body. The cephalic extremity is flattened and lips are absent. The triangular mouth opening is guarded by one dorsal and two thin subventral membranous cuticular flaps, the latter with fringed outer edges that project into the buccal cavity from the anterior end of the buccal capsule. The mouth opening is surrounded by six bean-shaped cuticular elevations, the two lateral ones bearing prominent amphids, the two ventral and two dorsal ones each with a cephalic papilla.

The oesophagus is 0.77 (0.51–0.77) long, nearly as wide as the bulbus. The isthmus is 0.48 (0.30–0.48) from the anterior end and the bulbus is 0.17 (0.10–0.17) long and 0.15 (0.11–0.15) wide. The intestine at the oesophago-intestinal junction is narrower than the bulbus. The nerve ring is 0.17 (0.15–0.18) from the anterior end, the prominent excretory pore 1.24 (0.80–1.24) and the vulva 2.98 (1.51–2.98), at the beginning of posterior third of the body.

A prominent pre-vulvar swelling is present and the short muscular ovejector has a distinct sphincter. The vagina is coiled, running anteriorly, joining the common uterus which turns posteriorly and divides into two uteri near the anus. The uteri run anteriorly, forming the oviducts near the mid-body. The blind ends of the ovaries both terminate near the excretory pore. Eggs are elongated, 0.129 long by 0.064 wide, thin shelled, and the terminal operculum is indistinct. Eggs are laid in an early stage of cleavage. The tail, tapering towards the posterior end, is slightly bent dorsally and is 0.33 (0.26–0.45) long.

HOST LOCALITY

Timbavati Private Game Reserve (24°0.5'51.4"S; 31°0.7'18.1"E), Northern Province, Republic of South Africa.

TYPE MATERIAL

Twenty females are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France, access number 294HS.

HABITAT

Stomach and large intestine.

Discussion

Contrary to the observations of Adamson & Nasher (1984), males and females *in copula* were not observed in this study. Furthermore, the key to the identification of the genera *Tachygonetria* and *Thelandros* (Petter & Quentin, 1976) is based on only the males and it was therefore impossible to identify the females with certainty to the species, or even the genus, level. Therefore the species were provisionally paired taking into consideration the anatomical similarities: *Tachygonetria bainae* with female Type C; *Tachygonetria chabaudi* with female Type A; *Tachygonetria petterae* with female Type D and *Thelandros schusteri*, *Thelandros boomkeri* or *Thelandros luciusi* with female Type E. Females Type B and F could not be paired. The morphological criteria employed were the length of oesophagus, the configuration of the cephalic papillae, the oesophago-intestinal junction and the length of the tail. Considering the difficulties with the identifications the pairings listed above should be treated with reserve

Since the Type E female could be paired to either *Thelandros schusteri*, *Thelandros boomkeri* or *Thelandros luciusi*, the possibility of male di- or polymorphism should also be considered (Jones 1992). Ainsworth (1990) originally described male dimorphism in two *Skrjabinodon* species (Pharyngodonidae) from New Zealand lizards. Furthermore, male polymorphism also occurs in the trichostrongylid subfamily Ostertagiinae (Lancaster & Hong 1981; Lichtenfels, Pilitt & Lancaster 1988; Andrews & Beveridge 1990; Stevenson, Gasser & Chilton 1996). However, whether male dimorphism does occur in the genus *Thelandros* is not clear. Because of the morphological differences between them, and until further studies prove the contrary, *Thelanddros schusteri*, *Thelandros boomkeri* and *Thelandros luciusi* should remain valid species.

The Pharyngodonidae seem to have evolved in two distinct lines, the one parasitic in insectivorous reptiles and the other in herbivorous ones (Petter 1966; Petter & Quentin 1976; Adamson 1981; Adamson

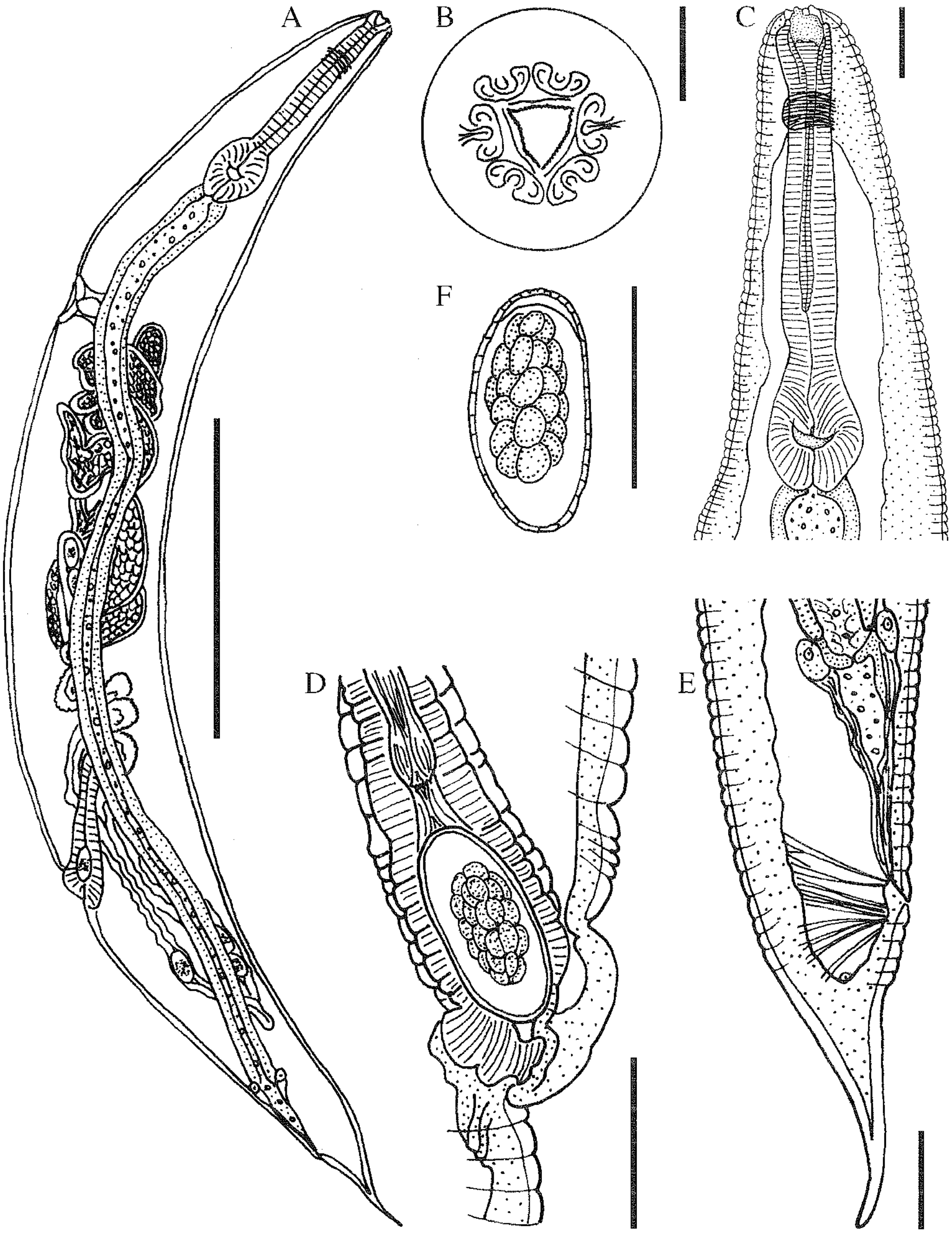

FIG. 12 Female type F

A	Lateral view of the entire nematode
B	Apical view of the head
C	Lateral view of the anterior region
D	Lateral view of the vulvar region. An egg is present in the ovejector
E	Lateral view of the posterior end
F	Egg

Scale bars: A—1 mm; C, D, E, F—0.1 mm; B—0.02 mm

& Nasher 1984). Adamson & Nasher (1984) emphasized that most of the radiation of the Pharyngodonidae of herbivorous reptiles probably took place in tortoises, which presumably have largely been herbivorous since their origin in the early and middle Eocene. Lizards are essentially insectivorous and a lineage of herbivorous lizards does not exist. Herbivorous and omnivorous feeding have only recently appeared in a number of isolated species. This is the case with *G. validus validus* which, unlike most other South African lizards, is omnivorous.

The richness and composition of the pharyngodonid fauna of *G. validus validus* is close to that of tortoises (Petter 1966). It differs from the pharyngodonid fauna of the insectivorous lizards that have been studied in which only the genera *Spauligodon*, *Skrjabinodon* and *Parapharyngodon* were recovered (Hering-Hagenbeck *et al.* 2002). The pharyngodonid fauna of *G. validus validus* seems to have originated by capture from local herbivorous reptiles. The three *Tachygonetria* spp. most closely resemble forms in South African tortoises (Petter, 1966). The three *Thelandros* spp. not only show strong similarities to those of herbivorous *Agama* spp. (Adamson & Nasher 1984), but also to those parasitic in tortoises and could have been acquired from either.

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Onderstepoort Journal of Veterinary Research, 73:111–114 (2006)

Gastric nematodes of Nile crocodiles, *Crocodylus niloticus* Laurenti, 1768, in the Okavango River, Botswana

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ABSTRACT

JUNKER, K., WALLACE, K., LESLIE, A.J. & BOOMKER, J. 2006. Gastric nematodes of Nile crocodiles, *Crocodylus niloticus* Laurenti, 1768, from the Okavango River, Botswana. *Onderstepoort Journal of Veterinary Research*, 73:111–114

The ascaridoid nematodes *Dujardinascaris madagascariensis* Chabaud & Caballero, 1966, *Dujardinascaris dujardini* (Travassos, 1920), *Gedoelstascaris vandenbrandeni* (Baylis, 1929) Sprent, 1978 and *Multicaecum agile* (Wedl, 1861) Baylis, 1923 were recovered from the stomach contents of *Crocodylus niloticus* Laurenti, 1768 from the Okavango River, Botswana, together with *Eustrongylides* sp., a dioctophymatoid nematode usually parasitizing piscivorous birds. *Dujardinascaris madagascariensis* was present in most of the infected hosts, while the remaining species were mostly represented in single collections in one to three hosts. All four ascaridoid nematodes represent new geographic records.

Keywords: Ascaridoidea, crocodilians, *Crocodylus niloticus*, nematodes, Nile crocodiles

INTRODUCTION

A number of gastrointestinal nematodes from crocodilian hosts have been reported in the literature (Baker 1983). Amongst these the ascaridoid nematodes belonging to the subfamily Heterocheilinae and Anisakinae are some of the most prominent species (Sprent 1977, 1978, 1979a, b).

Eight of the 11 genera are included in the subfamily Heterocheilinae parasitize crocodilians, namely *Brevimulticaecum* Mozgovoy, in Skrjabin, Shikhobalova & Mozgovoy, 1952, *Dujardinascaris* Baylis, 1947, *Gedoelstascaris* Sprent, 1978, *Hartwichia* Chabaud & Bain, 1966, *Multicaecum* Baylis, 1923, *Ortleppascaris* Sprent, 1978, *Trispiculascaris* Skrjabin, 1916 and *Typhlophorus* Von Linstow, 1906 (Sprent 1983). The genus *Terranova* Leiper & Atkinson, 1914 is included in the subfamily Anisakinae (Sprent 1979a).

The genera *Hartwichia* and *Trispiculascaris* have as yet only been recorded from the African continent, while *Brevimulticaecum* occurs in South and North American crocodilians, and *Typhlophorus* seems exclusive to India. *Gedoelstascaris* and *Multicaecum* have both been found in Africa and Australasia, whereas *Ortleppascaris* is known from African as well as South and North American hosts.

To date, *Terranova* and *Dujardinascaris* are the only ascaridoid genera occurring throughout the entire range of the crocodilians' geographic distribution, with representatives in the Neotropics, Africa and Australasia (Sprent 1977, 1978, 1979a, b, 1983). Even genera with a wide geographic distribution are generally characterized by strict species separation with respect to the various geographic areas. *Multi-*

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caecum agile (Wedl, 1861) Baylis, 1923 and *Terranova crocodilii* (Taylor, 1924) Hartwich, 1957, in fact, are the only two species that have been listed from Africa as well as Australia.

In this paper we report on some nematodes recovered from the stomach contents of Nile crocodiles, *Crocodylus niloticus* Laurenti, 1768, in Botswana.

MATERIAL AND METHODS

During August 2003 to August 2005 a study was conducted by one of us (K. Wallace) on the composition of the diet of Nile crocodiles from the Okavango River, Botswana. The stomach contents of the crocodiles were pumped into separate containers and macroscopically examined. Nematodes present in these contents were collected and fixed in 70 % ethanol. They were subsequently cleared in lactophenol and identified using the descriptions of the authors listed below. Nematodes were recovered from 57 crocodiles.

The results compiled herein are not based on a complete collection of the helminth parasites, for which the hosts would have had to be sacrificed, but represent incidental findings from the stomach contents of the various crocodile hosts.

RESULTS

The ascaridoids *Dujardinascaris madagascariensis* Chabaud & Caballero, 1966, *Dujardinascaris dujardini* (Travassos, 1920), *M. agile* and *Gedoelstascaris vandenbrandeni* (Baylis, 1929) Sprent, 1978 were recovered from the crocodiles. One male and one female specimen of the dioctophymatoid genus *Eustrongylides* Jägerskiöld, 1909 were present in a single host.

Helminth diversity was low in the Nile crocodiles examined, with the genus *Dujardinascaris* being the most commonly encountered. *Dujardinascaris madagascariensis* was recovered from most of the infected hosts, while the remaining species, *D. dujardini*, *G. vandenbrandeni* and *M. agile*, only occurred in a few (1–3) of the crocodiles.

The majority of the crocodiles (46) were only parasitized by one ascaridoid species, usually *Dujardinascaris madagascariensis*. Two of the ascaridoid species were present at the same time in only six hosts. Multiple infections with more than two species per host were not encountered.

DISCUSSION

While it is difficult to distinguish between some of the females of the various *Dujardinascaris* spp., *D. madagascariensis* is distinct from the other four African species in that the vagina opens through a distinct papilla between the lips of the vulva. In some of our specimens remains of copulatory cement could still be observed on the papilla. The majority of the male specimens were assigned to *D. madagascariensis* on the basis of the length of their spicules. The spicules of *D. dujardini* are distinctly longer than those of *D. madagascariensis*, whereas the spicules of both *Dujardinascaris gedoelsti* Sprent, 1977 and *Dujardinascaris puylaerti* Sprent, 1977 are considerably shorter (Sprent 1977). *Dujardinascaris petterae* Sprent, McKeown & Cremin, 1998 has short, unequal spicules (Sprent, McKeown & Cremin 1998). A single male specimen possessed the typical trifurcate gubernaculum of *D. dujardini* and a single female with a sinuous vagina, but without a vaginal papilla was assigned to the same species.

All the parasites reported in this study have previously been reported from crocodiles.

Dujardinascaris dujardini has been recorded from *C. niloticus* and *Crocodylus cataphractus* from Africa, as well as from *Crocodylus porosus* in India (Yamaguti 1961). Sprent (1977) lists "crocodile" as its type host and the Nile crocodile as additional host from Zambia and the Democratic Republic of the Congo. More recently, *D. dujardini* was reported from *C. niloticus* from Egypt (El-Dien Mahmoud 1999). *Dujardinasceris madagascariensis* is listed from *C. niloticus* and *C. cataphractus* in Madagascar, Angola and the Democratic Republic of the Congo (Sprent 1977). However, the recovery of *D. dujardini* and *D. madagascariensis* from crocodiles in Botswana represents a new geographic record for these parasites.

Three additional representatives of the genus *Dujardinascaris* have been reported from the African continent. Sprent *et al*. (1998) described *D. petterae* from *Osteolaemus tetraspis* in the Congo. *Dujardinascaris gedoelsti* Sprent, 1977 and *D. puylaerti* Sprent, 1977 were collected from *C. niloticus* in the Republic of the Congo (Sprent 1977). The latter species was also present in Zambia (Sprent 1977). None of the above three species was recovered from crocodiles in Botswana.

Gedoelstascaris vandenbrandeni is one of two species that Sprent (1978) removed from the genus *Dujardinascaris* and placed in a new genus, namely *Gedoelstascaris*. *Gedoelstascaris vandenbrandeni* occurs only in African crocodiles and has been recorded from *C. niloticus* and *C. cataphractus* in Angola, Zambia and the Democratic Republic of the Congo. Its Australian counterpart, *Gedoelstascaris australiensis* (Baylis 1931) Sprent, 1978, parasitizes *Crocodylus johnstoni* and *C. porosus* and has been found in hosts from Australia as well as the Solomon Islands (Sprent 1978). There are no previous records of *G. vandenbrandeni* in Botswana.

Of the four ascaridoid nematodes found in this study, *M. agile* is the only one with a geographic distribution extending beyond the African continent and utilizing hosts other than African crocodilians. Its type host is *C. niloticus* from Egypt, but it has also been recovered from *C. cataphractus* and was recorded from the Republic of the Congo, Zambia and Zimbabwe. Hosts from the Australasian region are *C. palustris*, *C. johnstoni* and *Gavialis gangeticus*. India and Australia are listed as localities (Sprent 1979b). Botswana constitutes a new geographic record for *M. agile*.

Literature regarding the prevalence and intensity of gastric nematode infections in crocodiles and alligators is scant and the data on both are somewhat variable (Cherry & Ager 1982; Ladds & Sims 1990; Goldberg, Bursey & Aquino-Shuster 1991). The latter might be explained by the fact that not many concise studies regarding the gastric nematode fauna of crocodilians have been conducted and findings often represent the data from few or single hosts.

Ladds & Sims (1990) report a prevalence of 41 % for *Dujardinascaris mawsonae* Sprent, 1977 in young crocodiles belonging to two species, *C. porosus* and *Crocodylus novaeguineae*, in Papua New Guinea. The range of intensity of infection is given as 1–20, but as many as 60 and 100 worms were recovered from two crocodiles in good condition. Histological examination of the gastric wall revealed the presence of *Capillaria* sp. in 60 % of the hosts.

Dujardinascaris waltoni Sprent, 1977 was the only nematode parasite present in *Alligator mississippiensis* in South Florida. It was collected from 93 % of the hosts and the mean intensity of infection was high (89 %), with a maximum burden of 413 specimens per alligator (Cherry & Ager 1982).

Contrary to our findings, *Dujardinascaris* was the least prevalent ascaridoid genus in *Caiman yacare* in Paraguay, but was nevertheless the one with the highest mean intensity of infection. *Brevimulticaecum baylisi* Travassos, 1933 had the highest prevalence followed by *Ortleppascaris alata* Baylis, 1947 (Goldberg *et al.* 1991). The genus *Brevimulticaecum* is exclusive to caimans and alligators in the New World (Sprent 1979). The genus *Ortleppascaris* is represented in Africa by a single species, *Ortleppascaris nigra* Gedoelst, 1916 from *C. niloticus* and *C. cataphractus* (Sprent 1978), but was not present in the crocodiles in Botswana.

No clear picture regarding the occurrence of multiple infections with ascaridoid nematodes emerges from the literature. Some authors report single species infections (Cherry & Ager 1982; Ladds & Sims 1990), while others list three or four species, without, however, specifying how many of these were recovered per individual host (Goldberg *et al.* 1991; Scott, Simcik & Craig 1997). Scott *et al.* (1997) examined the helminth fauna of 50 American alligators and came to the conclusion that the infracommunity structure was "depauperate when compared to homoiothermic hosts", a statement which complies with the well documented fact that the helminth diversity of reptiles, in general, is less pronounced than that of mammalian and avian hosts (Hering-Hagenbeck & Boomker 2000).

With the exception of *Eustrongylides* sp., all the parasites were collected from their typical predilection site in the host, but *D. dujardini*, *D. gedoelsti* and *G. vandenbrandeni* have also been reported from the intestine (Sprent 1977; Sprent *et al.* 1998). The genus *Eustrongylides* occurs in the wall of the proventriculus of its piscivorous avian final hosts and utilizes fish as intermediate hosts (Measures 1987).

Little is known about the life-cycle of any of the parasites found during this study, but fishes seem to play an important role as intermediate hosts of all the species (Sprent 1977, 1978, 1979a, b). Studies on the stomach contents of Nile crocodiles reveal a significant change in their feeding habits as the individuals grow larger. Despite this ontogenetic food-shift, fish remain one of the most important dietary items throughout the crocodiles' lifespan. Fish were found in the stomachs of 60 % of crocodiles ranging from 2.5–3.0 m in total length, and fish were still recovered from nearly 40 % of specimens >4.5 m, (Ross 1989; Alderton 1992). As one of the main prey items, fish would appear to be the intermediate host of choice to ensure the successful completion of the life-cycle of these gastric nematodes.

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Onderstepoort Journal of Veterinary Research, 73:315–317 (2006)

RESEARCH COMMUNICATION

Eustrongylides sp. (Nematoda: Dioctophymatoidea) from the stomach of a Nile crocodile, *Crocodylus niloticus* Laurenti, 1768, in Botswana

K. JUNKER[1], O. BAIN[2] and J. BOOMKER[1*]

ABSTRACT

JUNKER, K., BAIN, O. & BOOMKER, J. 2006 *Eustrongylides* sp. (Nematoda: Dioctophymatoidea) from the stomach of a Nile crocodile, *Crocodylus niloticus* Laurenti, 1768, in Botswana. *Onderstepoort Journal of Veterinary Research*, 73:315–317

During a study conducted between 2003 and 2005 on the diet of Nile crocodiles in Botswana, two young adult nematodes, one male and one female, belonging to the genus *Eustrongylides* Jägerskiöld, 1909 were recovered from the stomach contents of one of these animals. The caudal bursa of the male is present and the ejaculatory duct could be identified, but the spicule could not be seen. The vulva of the female has opened and the anus is situated on a terminal protruberance. Measurements and drawings of these specimens are provided, together with some data on the occurrence and life-cycles of members of the genus *Eustrongylides* in crocodilians world-wide and in African hosts in particular. Piscivorous birds are the usual final hosts of these nematodes. It is probable that the specimens described herein had developed in a paratenic fish host, and that the latter had been eaten by the crocodile.

Keywords: Botswana, *Crocodylus niloticus*, *Eustrongylides* sp., Nile crocodile???

During a study conducted between 2003 and 2005 on the composition of the diet of Nile crocodiles, *Crocodylus niloticus* Laurenti, 1768, in Botswana, nematode parasites were collected from their stomach contents and identified (Junker, Wallace, Leslie & Boomker 2006). Two large young adult specimens of the genus *Eustrongylides* Jägerskiöld, 1909, one male and one female, were recovered from a single crocodile only (Fig. 1).

The male is 110 mm long, 650 µm wide; posterior part with subterminal constriction; ventral precloacal sucker; caudal bursa with peripheral cuticular ornamentation, similar to that described for the genus (Karmanova 1968; Measures 1988a); ejaculatory duct identified but not the spicule.

The female is 122 mm long, 1 000 µm wide; vulva opened, close to anus; anus on a flattened terminal protruberance, which is 35 µm high.

The specimens are deposited at the Muséum National d'Histoire Naturelle Paris, Access number 169 JW.

This is a somewhat unusual finding since the genus *Eustrongylides* usually occurs in the wall of the proventriculus of its piscivorous avian final hosts and utilizes oligochaetes as intermediate hosts, in which it reaches the third larval stage (Anderson 2001). Fish subsequently serve as paratenic hosts in which the parasites reach the fourth stage and continue to grow. At this stage the reproductive system is highly developed (Measures 1988b; Anderson 2000). Coy-

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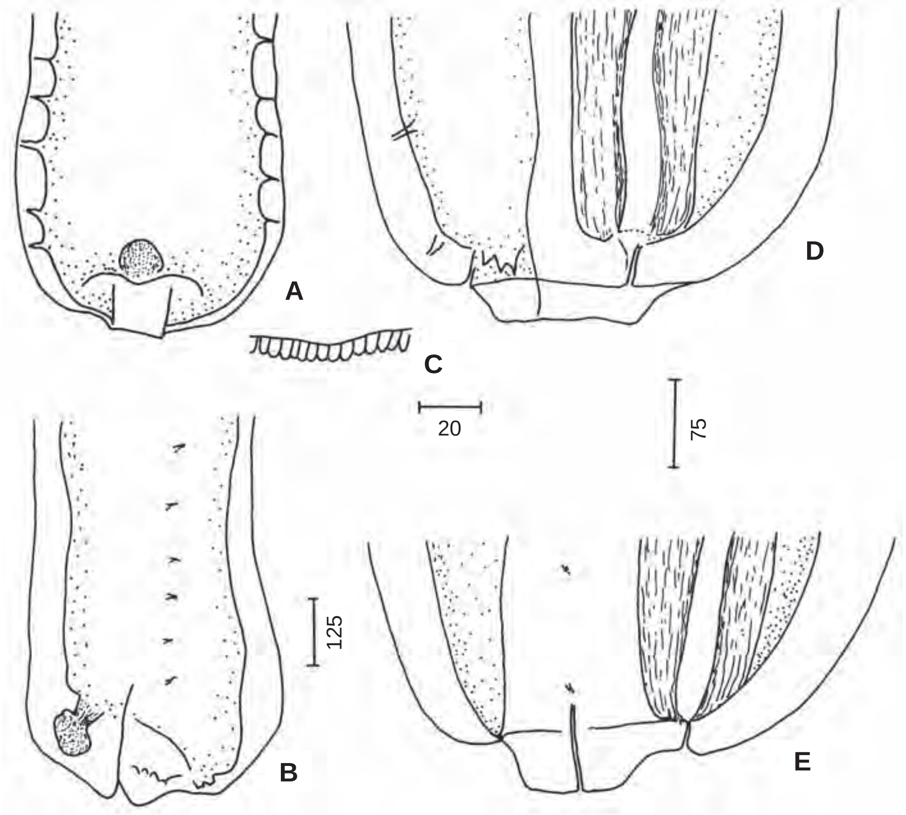

FIG. 1 *Eustrongylides* sp.. Caudal extremities of immature adults. A–C Male. A: Ventral view. B: Left lateral view. C: Internal peripheral ornamentation of the caudal sucker. D–E Female. D: Subventral view. E: Right lateral view. Note that the anus is situated on a terminal protruberance. Scales in µm: A, B = 125; C = 20; D, E = 75

ner, Spalding & Forrester (2002) found that fish could serve as intermediate as well as paratenic hosts for *Eustrongylides ignotus* Jägerskiöld, 1909.

Only a few publications refer to *Eustrongylides* sp. from crocodilian hosts. Ladds & Sims (1990) found immature *Eustrongylides* sp., 30–35 mm in length, free in the abdomen of two of 54 crocodiles in Papua New Guinea and Goldberg, Bursey & Aquino-Shuster (1991) report *Eustrongylides* sp. from the stomach contents of three of 115 wild-caught *Caiman yacare* (Daudin, 1802) in Paraguay. However, they could not determine whether the specimens of *Eustrongylides* they collected were recently released from intermediate host cysts and were likely to die, or whether they may have survived, with *C. yacare* becoming a paratenic host.

Similarly, our data is insufficient to decide whether the presence of *Eustrongylides* sp. in the stomach of the crocodile is accidental or represents an unusual life-cycle. Without the benefit of further life-cycle studies, it would appear as if the crocodile had ingested an infected fish and that the parasites were released from their host during the digestive process or had actively started migrating upon the death of their host. Considering that the specimens were adults, albeit immature, one could also speculate that the crocodile had ingested an infected waterbird. However, no remains of feathers were found in the stomach contents of the crocodile (Kevin Wallace, personal communication **date?**).

A substantial portion of the diet of Nile crocodiles, ranging from very small to large in size, is made up of fish, with aquatic birds also forming part of their diet (Ross 1989; Alderton 1999). It is thus not too surprising to find fish or bird parasites in a crocodile's stomach.

Little information is available on the prevalence of *Eustrongylides* in African paratenic as well as final hosts, and despite Measures' (1988a) revision of the genus, many taxonomic problems remain unsolved. She only confirmed three species, namely *Eustrongylides tubifex* (Nitzsch in Rudolphi, 1819) Jägerskiöld, 1909, *Eustrongylides excisus* Jägerskiöld, 1909 and

E. ignotus and declared nine species as *species inquirendae*.

A 26.5 % prevalence of larvae of *Eustrongylides africanus* Jägerskiöld, 1909, one of the species considered doubtful by Measures (1988a), and which is only known by the female, has been reported in catfish, *Clarias gariepinus* (Burchell, 1822) as well as *Clarias anguillaris* (Linnaeus, 1758), from the Bida floodplain of Nigeria (Ibiwoye, Balogun, Ogunsusi & Agbontale 2004). The latter authors indicate that fish can serve as intermediate, reservoir and as final hosts.

Eustrongylides africanus has also been recorded as part of the parasite fauna of two of six marabou storks, *Leptoptilus crumeniferus* (Lesson, 1831), in Uganda (Moriearty, Pomeroy & Wanjala 1972) as well as in *Ardea goliath* Cretzschmar, 1829, *Pelecanus rufescens* Gmelin, 1789, and *Anhinga melanogaster* (Daudin, 1802) in the Sudan (Measures 1988a).

Eustrongylides sp. has been recovered from fish at Lake Tana, Ethiopia (Eshetu & Enyew 2003). Asanji (1990) examined 2 576 *C. gariepinus* in Cameroon and found an overall prevalence of infection of 68.9 %. The latter author reports that cysts containing various larval stages were present in the muscles and visceral organs.

While the above indicates that *Eustrongylides* sp. is indeed quite common and wide-spread on the African continent, it equally emphasizes the paucity of data available on this parasite in Africa. It is to be hoped that an effort will be made to rectify this and to clarify the uncertain systematic status of, amongst others, *E. africanus*.

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Onderstepoort Journal of Veterinary Research, 67:1–13 (2000)

A check-list of the nematode parasites of South African Serpentes (snakes) and Sauria (lizards)

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ABSTRACT

HERING-HAGENBECK, S.F.B.N. & BOOMKER, J. 2000. A check-list on the nematode parasites of South African Serpentes (snakes) and Sauria (lizards). *Onderstepoort Journal of Veterinary Research*, 67:1–13

Published records, in combination with own data have been brought together to provide data on parasite/host relationships of reptiles that occur in the Republic of South Africa.

A total of 62 nematode species belonging to 23 genera and 11 families are recorded from 20 snake and 21 lizard species. The genera *Kalicephalus, Spauligodon, Ophidascaris* and *Abbreviata* are especially well represented with between five and eight species per genus. The most nematode species were recorded from the flap-neck chameleon, *Chamaeleo dilepis* (eight), the puff-adder, *Bitis arietans* (eight) and the water monitor, *Varanus niloticus* (seven). All synonyms of parasites and hosts are given.

Keywords: Lizards, nematodes, reptiles, snakes, South Africa

INTRODUCTION

More than 400 species of reptiles occur in South Africa in biomes that vary from the Western Cape macchia to the grasslands of the Free State, the mountainous highlands of KwaZulu-Natal and the arid regions of the Northern Cape. Their helminth parasites, however, have attracted little attention and few records exist in the literature. Those that do exist are mostly of a taxonomic nature and only a single one deals with a survey.

The aim of this check-list is to provide a source of reference to the original records of the nematodes of reptiles occurring in South Africa. Synonyms of the nematodes and their host species are provided. Only adult worms have been included and doubtful records or host identifications are indicated by a question mark (?). Records from reptiles that also have a distribution outside South Africa are included in this list.

We have partly followed Round's (1968) and Khalil & Polling's (1997) format and thus present the check-list in two parts. In the first part, the parasites are listed under their scientific names together with the synonyms and authorities, and the host and country from which the parasite was reported.

In the second part, the hosts are listed, together with their synonyms and their parasites, the latter in alphabetical order.

The system of classification of the nematodes conforms with the views held by Anderson, Chabaud & Willmott (1974–1983), while the classification and synonymies of the hosts are based on the works by Broadley (1983) and Branch (1998).

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PARASITE/HOST CHECK-LIST

Nematoda

Family RHABDIASIDAE Railliet, 1915

GENUS *RHABDIAS* STILES & HASSALL, 1905

1. *Rhabdias fuscovenosa* (Railliet, 1899) Goodey, 1924

Ascaris humilis Leidy, 1856; *Strongylus catanensis* Rizzo, 1902; *Rhabdias ophida* Goodey, 1924; *Rhabdias vellardi* Pereira *sensu* Harwood, 1932; *Rhabdias annulosa* Hsu, 1933

Bitis arietans
Fantham & Porter (1950), South Africa

Hemachatus haemachatus
Fantham & Porter (1950), South Africa

Naja nivea
Fantham & Porter (1950), South Africa

Family DIAPHANOCEPHALIDAE Travassos, 1920

GENUS *KALICEPHALUS* MOLIN, 1861

Subgenus *Kalicephalus* (*Variabiliformis*) Lichtenfels, 1980

1. *Kalicephalus colubri colubri* (Ortlepp, 1923) Lichtenfels, 1980

Kalicephalus minutus Boulenger, 1926; *Kalicephalus minutus* Fantham & Porter, 1950; *Kalicephalus obliquus* Schuurmans Stekhoven, 1937

Bitis arietans
Peirce (1984), Zambia
Schad (1962), Congo

Naja melanoleuca
Schad (1962), West Africa

Peudoaspis cana
Schad (1962), Kenya

2. *Kalicephalus paracolubri paracolubri* Ghadirian, 1968

Naja melanonleuca
Ghadirian (1968), Central African Republic

3. *Kalicephalus vipera obliquus* (Daubney, 1923)

Diaphanocephalus obliquus Daubney, 1923; *Kalicephalus obliquus* Ortlepp, 1923; *Kalicephalus bitisi* Campana-Rouget & Chabaud, 1950

Bitis arietans
Daubney (1923), Africa
Fantham & Porter (1950), South Africa

Bitis gabonica
Campana-Rouget & Chabaud (1950), Ivory Coast
Ortlepp (1923); Fantham & Porter (1950), South Africa

Causus rhombeatus
Daubney (1923), Africa
Fantham & Porter (1950), South Africa

Psammophylax tritaeniatus
Fantham & Porter (1950), South Africa

Subgenus *Kalicephalus* (*Schadius*) Lichtenfels, 1980

4. *Kalicephalus costatus micrurus* (Daubney, 1923) Schad, 1962

Diaphanocephalus micrurus Daubney, 1923; *Kalicephalus micrurus* Yorke & Maplestone, 1926

Crotaphopeltis hotamboeia
This paper, South Africa
Wahid (1961), Malawi

Dispholidus typus
Schad (1962), London Zoo

Macrelaps microlepidotus
Daubney (1923); Baylis (1929), South Africa

5. *Kalicephalus simus simus* (Daubney, 1923) Yorke & Maplestone, 1926

Kalicephalus nigeriensis Ortlepp, 1923

Dendroaspis angusticeps
Fantham & Porter (1950), South Africa

Dendroaspis polylepis
Ortlepp (1926) in Schad (1962), Congo

Naja melanoleuca
Van den Berghe (1943); Schad (1962), Congo

Naja mossambica
Peirce (1984), Zambia
Fantham & Porter (1950), South Africa

Psammophis brevirostris
Fantham & Porter (1950), South Africa

Species inquirendae (After Schad 1962)

6. *Kalicephalus rotundatus* v. Linstow, 1908

Pseudoaspis cana
Von Linstow (1908), South Africa

Family PHARYNGODONIDAE Travassos, 1919

GENUS *PARAPHARYNGODON* CHATTERJI, 1933

1. *Parapharyngodon rotundatus* (Malan, 1939) Freitas, 1957

Thelandros rotundatus Malan, 1939

Agama atra
Malan (1939); Freitas (1957), South Africa

Pseudocordylus microlepidotus
Malan (1939); Freitas (1957), South Africa

GENUS *PHARYNGODON* DIESING, 1861

Neopharyngodon Chakravarty & Bhaduri, 1948

1. *Pharyngodon* sp.

Agama aculeata aculeata
Heideman (1995), Namibia

GENUS *SPAULIGODON* SKRJABIN, SCHIKHOBALOVA & LAGODOVSKAJA, 1960

1. *Spauligodon auziensis* (Seurat, 1917) Skrjabin *et al.*, 1960

Hemidactylus mabouia
Moravec *et al.* (1987), Egypt

2. *Spauligodon morgani* (Fitzsimmons, 1961) Barus & Coy Otero, 1974

Pharyngodon morgani Fitzsimmons, 1961

Hemidactylus mabouia
Simonsen & Sarda (1985), Tanzania

Mabuya quinquetaeniata
Simbotwe (1979), Zambia

Mabuya striata
Fitzsimmons (1961), Malawi
Simbotwe (1979), Zambia

3. *Spauligodon petersi* Bursey, McAllister & Freed, 1997

Mabuya sulcata sulcata
Bursey *et al.* (1997), South Africa

4. *Spauligodon smithi* Bursey, McAllister & Freed, 1997

Pachydactylus bibronii
Bursey *et al.* (1997), South Africa

5. *Spauligodon timbavatiensis* Hering-Hagenbeck & Boomker, 1998

Pachydactylus turneri
Hering-Hagenbeck & Boomker (1998), South Africa

6. *Spauligodon vojteki* Moravec, Barus & Rysavy, 1987

Mabuya quinquetaeniata
Moravec *et al.* (1987), Egypt

GENUS *THELANDROS* WEDL, 1862

Avilandros Skrjabin, Schikhobalova & Mozgovoi, 1951

1. *Thelandros alatus* Wedl, 1862

Oxyuris uromasticola Galeb, 1889; *Thelandros micruris* Rauther, 1918; *Thelandros sahariensis* Baylis, 1930; *Thelandros avis* Maplestone, 1940

Agama mossambica
Myers *et al.* (1960), Sudan

GENUS *SKRJABINODON* INGLIS, 1968

1. *Skrjabinodon dossae* (Caballero, 1968) Schmidt & Kuntz, 1972

Hemidactylus mabouia
Schmidt & Kuntz (1972), Madagascar

2. *Skrjabinodon mabuyae* (Sandground, 1936) Inglis, 1968

Mabuya varia
Baker (1987), Uganda

3. *Skrjabinodon mabuiensis* (Malan, 1939) Inglis, 1968

Pharyngodon mabuiensis Malan, 1939

Mabuya striata
Malan (1939), South Africa

Family COSMOCERCIDAE Travassos, 1925

Subfamily Cosmocercinae Railliet, 1916

GENUS *APLECTANA* RAILLIET & HENRY, 1916

1. *Aplectana macintoshii* (Stewart, 1914) Travassos, 1931

Aplectana agubernaculum Gupta, 1960; *Aplectana asiatica* Gupta, 1960; *Aplectana schneideri* Travassos, 1931; *Aplectana stormi* Travassos, 1931; *Aplectana varelai* Rodrigues, Rodrigues & Cristofaro, 1972; *Ascaris commutata* Diesing, 1851 *sensu* Claparede, 1859; *Neyraplectana ranae* Wang, Zhao & Chen, 1978; *Neoraillietnema ranae* Wang, 1980; *Neoraillietnema praeputiale* Skrjabin, 1916; *Nematoxys commutatus* Rudolphi *sensu* Schneider, 1866; *Oxysomatium stomatici* Biswas & Chakravarty, 1963; *Oxysomatium longicaudata* Yuen, 1965; *Oxysomatium minutum* Rasheed, 1965; *Oxysomatium macintoshii kirtipuri* Singh, 1969; *Oxysomatium mehdii* Ilyas, 1980; *Raillietnema praeputiale* (Skrjabin, 1916) *sensu* Kozak, 1969; Deshmukh, 1970; Vojtkova, 1976

Varanus niloticus
Rasheed (1965), Cameroon

Varanus niloticus
Baker (1980), Sudan

Family HETERAKIDAE Railliet & Henry, 1912

Subfamily Spinicaudinae Travassos, 1920

GENUS *AFRICANA* TRAVASSOS, 1920

Preterakis Freitas, 1956

1. *Africana acuticeps* (Gedoelst, 1916) Travassos, 1920

   Chamaeleo dilepis
   Baylis (1937), Congo

2. *Africana africana* (Gendre, 1909) Travassos, 1920

   Varanus niloticus
   Graber (1981), Congo

GENUS *STRONGYLURIS* MUELLER, 1894

1. *Strongyluris brevicaudata* Mueller, 1894

   Agama sp.
   Cowper (1969), Nigeria

   Bradypodion pumila
   Boomker & Petter (unpublished), South Africa

   Chamaeleo dilepis
   Schmidt & Canaris (1968), Kenya
   Sand-ground (1928), Tanzania

2. *Strongyluris capensis* Pruedhoe & Harris, 1971

   Bradypodion pumila pumila
   Prudhoe & Harris (1971), South Africa

3. *Strongyluris elegans* (Gendre, 1909) Railliet & Henry, 1914

   Chamaeleo dilepis
   Gedoelst (1916), Congo

4. *Strongyluris ornata* (v. Linstow, 1897) Railliet & Henry, 1914

   Acanthocerus atricollis
   Harwood (1935), Tanzania

   Agama atra
   This paper, South Africa

Family ASCARIDIDAE Baird, 1853

GENUS *HEXAMETRA* TRAVASSOS, 1919

1. *Hexametra applanata* (v. Linstow, 1899) Sprent, 1978

   Chamaeleo dilepis
   Gedoelst (1916), Zaire

2. *Hexametra hexametra* (Gedoelst, 1916) Travassos, 1920

   Chamaeleo dilepis
   Sprent (1978), Zaire
   Baylis (1920), Congo
   Cowper (1969), Nigeria

3. *Hexametra quadricornis* (Wedl, 1861) Kreis, 1944

   Ascaris gestri Parona, 1889; *Ascaris quadrilobata* v. Linstow, 1908; *Hexametra anguinea* Wu & Hu, 1938; *Hexametra daelhlholtzlii* Kreis, 1944; *Hexametra multicornis* Mozgovoi & Romanova 1970; *Hexametra boskovi* Moravec, 1966; *Hexametra skrjabini* Markov, Bogdanov & Persianova, 1970; *Hexametra dagestanica* Markov, Khonyakina & Grigor´eva, 1972; *Ophidascaris natricis* Yamaguti, 1935; *Ophidascaris genoheteromegala* Kreis, 1938; *Ophidascaris microspicula* Kreis, 1938; *Polydelphis waterstoni* Baylis, 1921; *Polydelphis sewelli* Baylis & Daubney, 1922; *Polydelphis dalmatina* Kreis, 1940; *Polydelphis najae* Mozgovoi, 1953

   Bitis arietans
   Fantham & Porter (1950), South Africa
   Baylis (1920); Sprent (1978), Africa

   Bitis gabonica
   Fantham & Porter (1950), South Africa
   Sprent (1978), Africa

   Causus rhombeatus
   Fantham & Porter (1950), South Africa

   Lamprophis fuliginosus
   Fantham & Porter (1950), South Africa

   Naja melanoleuca
   Fantham & Porter (1950), Malawi
   Sprent (1978), Africa

   Naja nigricollis
   Sprent (1978), Africa

   Psammophis subtaeniatus
   Wahid (1961), Zimbabwe

   Pseudoaspis cana
   Baylis (1920); Sprent (1978), Africa
   Fantham & Porter (1950), South Africa

   Python sebae
   Sprent (1978), Africa

GENUS *OPHIDASCARIS* BAYLIS, 1920

1. *Ophidascaris amucornata* Schuurmans Stekhoven, 1937

   Python sebae
   Sprent & McKeown (1979), Kenya

2. *Ophidascaris filaria* (Dujardin, 1845) Baylis, 1920

   Ascaris rubicunda Schneider, 1866; *Ophidascaris ajarensis* Khera, 1954, *pro parte*

   Lamprophis fuliginosus
   Fantham & Porter (1950), South Africa

   Naja melanoleuca
   Fantham & Porter (1950), Malawi

   Python sebae
   Aruo (1977) in Baker (1987), Uganda
   Baylis (1920), Zanzibar
   Fantham & Porter (1950), South Africa

3. *Ophidascaris intorta* (Gedoelst, 1916) Baylis, 1920

   Bitis arietans
   Fantham & Porter (1950), South Africa

Bitis gabonica
Fantham & Porter (1950), South Africa

4. *Ophidascaris mombasica* Baylis, 1921

Lycodonomorphus rufulus
Fantham & Porter (1950), South Africa

Psammophis subtaeniatus
Baylis (1920), Kenya

5. *Ophidascaris naiae* (Gedoelst, 1916) Baylis, 1920

Ophidascaris daubaylisi Baylis & Daubney, 1922; 1923

Naja mossambica
Fantham & Porter (1950), South Africa

Naja nivea
Fantham & Porter (1950), South Africa

"Python"
Bwangamoi (1968), Uganda

6. *Ophidascaris radiosa* (Schneider, 1866) Baylis, 1920

Bitis gabonica
Baylis (1920), Africa

Causus rhombeatus
Fantham& Porter (1950), South Africa

GENUS *ORNEOASCARIS* SKRJABIN, 1916

Amplicaecum Baylis, 1920

1. *Orneoascaris chrysanthemoides* Skrjabin, 1916

Ascaris involuta Gedoelst, 1916; *Ascaris bufonis* Gedoelst, 1916 *nec* Schrank, 1788; *Ascaris colura* Baylis, 1919; *Amplicaecum africanum* Taylor, 1924; *Amplicaecum causi* Thwaite, 1926; *Amplicaecum gedoelsti* Yorke & Maplestone, 1926; *Amplicaecum novempapillatum* Sandground, 1933; *Amplicaecum pesteri* Rasheed, 1965

Bitis cornuta
Vuylsteke (1964), Central Africa

Causus rhombeatus
Fantham & Porter (1950), South Africa

Chamaeleo dilepis
Thwaite (1926), Africa

Dispholydus typus
Rasheed (1965), Cameroon

2. *Orneoascaris schoutedeni* (Baylis, 1940) Le Van Hoa, 1960

Varanus albigularis
Sprent (1985a), Tanzania

Varanus niloticus
Le Van Hoa (1960), Zaire

GENUS *POLYDELPHIS* DUJARDIN, 1845

1. *Polydelphis anoura* Dujardin, 1845

Ascaris attenuata Molin, 1858; *Ascaris oculata* v. Linstow, 1899; *Ascaris pythonis* Retzius, 1830; *Ascaris rubicunda* Schneider, 1866 (*pro parte*); *Polydelphis bicornuta* Robinson, 1934; *Polydelphis mucronata* Panagia, 1933

Bitis arietans
Von Linstow (1899), South Africa

Python sebae
Fantham & Porter (1950), South Africa
Baylis (1940), Congo
Peirce (1984), Zambia

GENUS *RAILLIETASCARIS* SPRENT, 1935

1. *Raillietascaris varani* (Baylis & Daubney, 1922) Sprent, 1935

Amplicaecum monitor Khera, 1954; *Amplicaecum iguanae* Wahid, 1961; *Amplicaecum mackerrasae* Thomas, 1959

Varanus niloticus
Sprent (1985b), Congo

Family GNATHOSTOMATIDAE Railliet, 1915

GENUS *TANQUA* BLANCHARD, 1904

Ctenocephalus v. Linstow, 1904; *Tetradenos* v. Linstow, 1904; *Anomala* Travassos, 1920

1. *Tanqua tiara* (v. Linstow, 1879) Blanchard, 1904

Varanus albigularis
Baylis (1939), South Africa

Varanus niloticus
Sandground (1933), Tanzania
Baylis & Lane 1920), Zanzibar
Gretillat & Gaillard (1966), Senegal

Family PHYSALOPTERIDAE (Railliet, 1893) Leiper, 1908

GENUS *ABBREVIATA* TRAVASSOS, 1920

Polydelphyoptera Schultz,1927; *Didelphyoptera* Schultz, 1927

1. *Abbreviata affinis* (Gedoelst, 1916) Chabaud, 1956

Crotaphopeltis hotamboeia
Chabaud (1956), Congo

Psammophis brevirostris
Fantham & Porter (1950), South Africa

2. *Abbreviata baylisi* Chabaud, 1956

Physaloptera quadrovaria Leiper, 1908; *Physaloptera paradoxa* v. Linstow, 1908

Varanus albigularis (?)
Chabaud (1956), Central Africa

3. *Abbreviata damarensis* Prudhoe & Harris, 1971

   Chamaeleo namaquensis
   Prudhoe & Harris (1971), Namibia

4. *Abbreviata nyassae* Fitzsimmons, 1964

   Aconthocercus atricollis
   Fitzsimmons (1964), Malawi

5. *Abbreviata ortleppi ortleppi* (Sandground, 1928) Morgan, 1945

   Chamaeleo dilepis
   Sandground (1928), Tanzania
   Morgan (1945), Tanzania

6. *Abbreviata polydentata* (Walton, 1932) Morgan, 1945

   Hemidactylus mabouia
   Morgan (1945), Tanzania

7. *Abbreviata quadrovaria* (Leiper, 1908) Schultz, 1927

   Varanus niloticus
   Ortlepp (1922), Sudan

8. *Abbreviata* sp.

   Agama aculeata
   Heideman (1995), Namibia

GENUS *SKRJABINOPTERA* SCHULTZ, 1927

Didelphysoma Schultz, 1927

1. *Skrjabinoptera chamaeleontis* (Gedoelst, 1916) Schultz, 1927

   Chamaeleo dilepis
   Vuylsteke (1964), Congo

2. *Skrjabinoptera simplicidens* (Ortlepp, 1922) Schultz, 1927

   Unidentified lizard
   Schultz (1927), South Africa

3. *Skrjabinoptera wetzeli* Hörchner & Weissenburg, 1965

   Agama hispida (?)
   Hörchner & Weissenburg (1965), Congo

   Agama hispida
   Simbotwe (1979), Zambia

GENUS *THUBUNAEA* SEURAT, 1914

1. *Thubunaea fitzsimmonsi* Ortlepp, 1931

   Ichnotropis squamulosa
   Ortlepp (1931), South Africa

GENUS *PHYSALOPTEROIDES* WU & LIU, 1940

Thubunaea Seurat,1914 (*pro parte*)

1. *Physalopteroides agamae* (Sandground, 1933) Chabaud & Brygoo, 1960

   Agama hispida
   Chabaud & Brygoo (1960), Mozambique

2. *Physalopteroides asymmetrica* (Baylis, 1930) Chabaud & Brygoo, 1960

   Hemidactylus mabouia
   Simonsen & Sarda (1985), Tanzania

3. *Physalopteroides grayicola* (Sandground, 1933) Chabaud & Brygoo, 1960

   Bitis arietans
   Chabaud & Brygoo (1960), Africa

4. *Physalopteroides impar impar* (Malan, 1939) Chabaud & Brygoo, 1960

   Agama atra
   Malan (1939); Chabaud & Brygoo (1960), South Africa

   Cordylus cordylus
   Chabaud & Brygoo (1960), South Africa

Family RHABDOCHONIDAE (Travassos, Artigas & Pereira, 1928) Skrjabin, 1946

GENUS *RHABDOCHONA* RAILLIET, 1916

Ichthyospirura Skrjabin, 1917; *Pseudorhabdochona* Liu & Wu, 1941; *Rhabdochonoides* Janizewska, 1955

1. *Rhabdochona puylaerti* Moravec, 1983

   Causus rhombeatus
   Moravec (1983), Uganda

Family DIPLOTRIAENIDAE (Skrjabin, 1916 subfam.) Anderson, 1958

GENUS *HASTOSPICULUM* SKRJABIN, 1923

Setarospiculum Mirza & Basir, 1939

1. *Hastospiculum macrophallos* (Parona, 1889) Baylis, 1930

   Filaria varani Baylis & Daubney 1922; *Hastospiculum spinigerum* Chandler, 1929; *Setarospiculum varani* Mirza & Basir, 1939; *Hastospiculum indicum* Yamaguti, 1961

   Varanus niloticus
   Thurston (1971), Uganda
   Gretillat & Gaillard (1966), Senegal

Family ONCHOCERCIDAE Leiper, 1911

Dipetalonematidae Wehr, 1935; Setariidae Yorke & Maplestone, 1926 subfam.

GENUS *BEFILARIA* CHABAUD, ANDERSON & BRYGOO, 1959

1. *Befilaria pseudocordyli* Gibbons, 1989

   Pseudocordylus microlepidotus
   Gibbons (1989), South Africa

GENUS *MADATHAMUGADIA* CHABAUD, ANDERSON & BRYGOO, 1959

1. *Madathamugadia hiepei* Hering-Hagenbeck, Boomker, Petit, Killick-Kendrick & Bain, 1999

   Pachydactylus turneri
   Hering-Hagenbeck *et al.* (1999), South Africa

2. *Madathamugadia ineichi* Bain, Wanji, Petit, Paperna & Finkelman, 1993

   Pseudocordylus microlepidotus
   Bain *et al.* (1993), South Africa

3. *Madathamugadia versterae* Bain, Wanji, Petit, Paperna & Finkelman, 1993

   Mabuya quinquetaeniata margaritifer
   Bain *et al.* (1993), South Africa

HOST/PARASITE CHECK-LIST

Serpentes

Family ATRACTASPIDIDAE (African burrowing snakes)

GENUS *MACRELAPS*

1. *Macrelaps microlepidotus* (Günther, 1860) (Natal blacksnake)

   Uriechis microlepidotus Günther, 1860; *Atractaspis natalensis* Peters, 1877; *Macrelaps microlepidotus* Boulenger, 1896

   Kalicephalus costatus micrurus

Family BOIDAE (Boas and phythons)

GENUS *PYTHON*

1. *Python sebae* A. Smith, 1840 (African rock python)

   Python natalensis A. Smith, 1840; *Hortulia natalensis* Gray, 1842

   Hexametra quadricornis
   Ophidascaris amucronata
   Ophidascaris filaria
   Polydelphis anoura

Family VIPERIDAE (Vipers)

GENUS *BITIS*

1. *Bitis arietans* (Merrem, 1820) Günther, 1858 (Puff-adder)

   Cobra lachesis Laurenti, 1768; *Cobra clotho* Laurenti, 1768; *Coluber lachesis* Gmelin, 1788; *Coluber bitin* Bonnaterre, 1789; *Coluber intumescens* Donndorf, 1798; *Vipera* (*Echidna*) *arietans* Merrem, 1820; *Vipera inflata* Burchell, 1822; *Echidna arietans* Wagler, 1828; *Vipera brachyura* Cuvier, 1829; *Clotho arietans* Gray, 1842; *Clotho lateristriga* Gray, 1842; *Echidna clotho* Steindachner, 1867; *Bitis lachesis* Bogert, 1940

   Hexametra quadricornis
   Kalicephalus colubri colubri
   Kalicephalus viperae obliquus
   Ophidascaris intorta
   Ophidascaris amucronata
   Physalopteroides grayicola
   Polydelphis anoura
   Rhabdias fuscovenosa

2. *Bitis gabonica* (Duméril & Bibron, 1854) Boulenger, 1896 (Gaboon adder)

   Cerastes nasicornis (*non* Shaw) Hallowell, 1847; *Echidna gabonica* Duméril & Bibron, 1854; *Bitis rhinoceros* (*non* Schlegel) Peters, 1882; *Cobra gabonica* Mertens, 1937

   Hexametra quadricornis
   Kalicephalus viperae obliquus
   Ophidascaris radiosa
   Ophidascaris intorta

3. *Bitis cornuta* (Daudin, 1803) (Many-horned adder)

   Verpera cornuta Daudin, 1803; *Vipera lophophris* Couvier, 1929; *Cerastes cornuta* Gray, 1842; *Vipera lophophrys* A. Smith, 1843; *Clotho cornuta* Gray, 1849; *Cerastes lophophrys* Duméril & Bibron, 1854; *Cobra cornuta* Mertens, 1937; *Bitis cornuta* Boulenger, 1896

   Orneoascaris chrysanthemoides

GENUS *CAUSUS*

1. *Causus rhombeatus* (Lichtenstein, 1823) Wagler, 1830 (Rhombic night-adder)

   Sepedon rhombeata Lichtenstein, 1823; *Aspidelaps rhombeatus* Jan, 1859; *Causus rhombeatus* var. *taeniata* Sternfeld, 1912

   Hexametra quadricornis
   Kalicephalus viperae obliquus
   Ophidascaris radiosa
   Orneoascaris chrysanthemoides
   Rhabdochona puylaerti

Family COLUBRIDAE (Typical snakes)

GENUS *LAMPROPHIS*

1. *Lamprophis fuliginosus* (Boie, 1827) Broadley, 1983 (Brown house-snake)

Lycodon fuliginosus Boie, 1827; *Lycodon geometricus* (*non* Schlegel) A. Smith, 1843; *Boaedon lineatum* (*pro parte, non* Duméril & Bibron) Günther, 1858; *Boaedon capense* Duméril & Bibron 1854; *Alopecion variegatum* Bocage, 1867; *Boodon quadrilineatus* Peters, 1867; *Boaedon quadrilineatus* var. *variegata* Jan, 1870; *Boodon geometricus* Fischer, 1888; *Boodon bipraeocularis* Günther, 1888; *Boodon mentalis* Günther, 1888; *Boodon lineatus* (*pro parte*) Boulenger, 1893; *Boaedon lineatus* Cott, 1935; *Boaedon mentalis* Rose, 1950; *Boaedon fuliginosus* Pitman, 1958

Hexametra quadricornis
Ophidascaris filaria

GENUS *LYCODONOMORPHUS*

1. *Lycodonomorphus rufulus* (Lichtenstein, 1823) Loveridge, 1953 (Common brown water-snake)

Coluber rufulus Lichtenstein, 1823; *Coronella leucopilus* A. Smith, 1831; *Coronella rufula* Schlegel (*pro parte*), 1837; *Lycodonomorphus rufula* Fitzinger, 1843; *Lamprophis rufulus* A. Smith, 1847; *Alabes rufula* Duméril & Bibron, 1854; *Ablabophis rufulus* Boulenger, 1893

Ophidascaris mombasica

GENUS *PSEUDOASPIS*

1. *Pseudoaspis cana* (Linnaeus, 1754) Cope, 1864 (Mole snake)

Coluber cana Linnaeus, 1754; *Coluber elegantissimus* Laurenti, 1768; *Coluber ocellatus* Gmelin, 1789; *Duberria cana* Fitzinger, 1826; *Coronella cana* Dumérgil & Bibron, 1854; *Cadmus cuneiformis* Theobald, 1868; *Coronella phocarum* Günther, 1872; *Ophirhina anchietae* Bocage, 1882; *Dasypeltis scabra* (*nec* Linnaeus) Gaerdes, 1962

Hexametra quadricornis
Kalicephalus colubri colubri
Kalicephalus rotundatus

GENUS *PSAMMOPHIS*

1. *Psammophis brevirostris* (Peters, 1881) Brandstädter, 1996 (Short-snouted grass-snake)

Psammophis sibilans sibilans (*non* Linnaeus) FitzSimmons, 1970; *Psammophis sibilans brevirostris* Broadley, 1977; *Psammophis brevirostris* Brandstädter, 1996

Abbreviata affinis
Kalicephalus simus simus

2. *Psammophis subtaeniatus* (Peters, 1882) Boulanger, 1896 (Stripe-bellied sand-snake)

Psammophis moniliger Peters (*pro parte, non* Daudin), 1854; *Psammophis sibilans* var. *bilineatus* Peters, 1867; *Psammophis sibilans* var. *subtaeniata* Peters, 1882; *Psammophis bocagii* Boulenger, 1896; *Psammophis transvaalensis* Gough, 1908; *Psammophis notostictus* (*non* Peters) Isemonger, 1955

Hexametra quadricornis
Ophidascaris mombasica

GENUS *PSAMMOPHYLAX*

1. *Psammophylax tritaeniatus* (Günther, 1868) Loveridge, 1953 (Striped skaapsteker)

Rhagerrhis tritaeniatus Günther, 1868; *Coronella tritaeniata* Günther, 1881; *Trimerorhinus tritaeniatus* Boulenger (*pro parte*) 1896; *Cerastes tritaeniatus* Gaerdes, 1962

Kalicephalus obliquus

GENUS *CROTAPHOPELTIS*

1. *Crotaphopeltis hotamboeia* (Laurenti, 1768) Barbour & Amaral, 1927 (Herald snake)

Coronella hotamboeia Laurenti, 1768; *Coronella virginica* Laurenti, 1768; *Coluber rufescens* Gmelin, 1789; *Coluber hitamboeia* Gmelin, 1789; *Coluber bicolor* Leach, 1819; *Ophis heterurus* Duvernoy, 1833; *Ophis albocinctus* Duvernoy, 1833; *Coronella rufescens* Schlegel, 1837; *Crotaphopeltis rufescens* A. Smith, 1849; *Dipsas inornatus* A. Smith 1849; *Heterurus rufescens* Duméril & Bibron, 1854; *Leptodeira rufescens* Günther, 1858; *Oxyropus melanocrotaphos* Cope, 1860; *Crotaphopeltis hitamboeia* Peters, 1882; *Leptodira rufescens* Boettger, 1887; *Leptodira hotamboeia* Boulenger, 1896; *Leptodira hitamboeia* Werner, 1898; *Leptodira hotamboeia* Flower, 1929; *Trabophis barnumbrowni* Bogert, 1940

Abbreviata affinis
Kalicephalus costatus micrurus

GENUS DISPHOLIDUS

1. *Dispholidus typus* (A. Smith, 1829) (Boomslang)

Bucephalus typus A. Smith, 1829; *Bucephalus jardinii, Bucephalus gutturalis, Bucephalus bellii* A. Smith, 1829; *Dispholidus lalandii* Duvernoy, 1832; *Dendrophis colubrina* Schlegel, 1837; *Bucephalus viridis* A. Smith, 1841; *Bucephalus capensis* A. Smith, 1841; *Dendrophis pseudodipsas* Bianconi, 1848; *Dispholidus typicus* Boulenger, 1896; *Thrasops jacksonii mossambicus* Mertens, 1937; *Dispholidus typicus* Boulenger, 1896

Kalicephalus costatus micrurus
Orneoascaris chrysanthemoides

Family ELAPHIDAE (Cobras, mambas and their relatives)

GENUS *DENDROASPIS*

1. *Dendroaspis angusticeps* (A. Smith, 1849) Hewitt, 1937 (Green mamba)

Naia angusticeps A. Smith, 1849; *Dendraspis angusticeps* Günther (*pro parte*), 1858; *Dendroaspis intermedius* Günther, 1865; *Dendroaspis sjöstedti* Lönnberg, 1907

Kalicephalus simus simus

2. *Dendroaspis polylepis* (Günther, 1864) FitzSimmons, 1946 (Black mamba)

Naia angusticeps A. Smith, 1849; *Chloroechis angusticeps* (*non* A. Smith) Peters, 1854; *Dendraspis angusticeps* (*non* A. Smith) Günther (*pro parte*), 1858; *Dendraspis polylepis* Günther, 1864; *Dendraspis antinorii* Peters, 1873; *Dinophis angusticeps* Peters, 1882; *Dendraspis mamba* Gough, 1908; *Dendroaspis angusticeps* (*non* A. Smith) Flower, 1937; *Dendroaspis mamba* Rose, 1950

Kalicephalus simus simus

GENUS *HEMACHATUS*

1. *Hemachatus haemachatus* (Lacépède, 1788) Stejneger, 1936 (rinkhals)

Vipere haemachate Lacépède, 1788; *Coluber haemachata* Lacépède, 1789; *Coluber haemachates* Bonnaterre, 1789; *Vipera haemachates* Latreille, 1802; *Sepedon haemachates* Merrem, 1820; *Naia capensis* A. Smith, 1826; *Naja haemachates* Schlegel, 1837; *Aspidelaps haemachates* Jan, 1863; *Sepedon haemachata* Flower, 1929; *Haemachatus haemachates* FitzSimmons, 1946

Rhabdias fuscovenosa

GENUS *NAJA*

1. *Naja melanoleuca* Hallowell, 1857 (Forest cobra)

Naja haje var *melanoleuca* Hallowell, 1857; *Aspidelaps bocagii* Sauvage, 1884; *Naja haje* var. *leucosticta* Fischer, 1885; *Naia melanoleuca* Boulenger, 1896; *Naja melanoleuca* Bogert, 1942

Hexametra quadricornis
Kalicephalus colubri colubri
Kalicephalus paracolubri paracolubri
Kalicephalus simus simus
Ophidascaris filaria

2. *Naja mossambica* Peters, 1854 (Mozambique spitting cobra)

Naja mossambica Peters, 1854; *Naja nigricollis* (*non* Reinhardt) Peters, 1882; *Naia nigricollis* Boulenger, 1898; *Naia nigricollis* var. *mossambica* Boulenger, 1896; *Naja nigricollis mossambica* Mertens, 1937; *Naja mossambica* Broadley, 1968

Ophidascaris naiae
Kalicephalus simus simus

3. *Naja nivea* (Linnaeus, 1758) Boie, 1827 (Cape cobra)

Coluber niveus Linnaeus, 1758; *Vipera* (*Echidna*) *flava* Merrem, 1820; *Naja haje* var. Schlegel, 1837; *Naja gutturalis* A. Smith, 1838; *Naja intermixta* Duméril & Bibron, 1854; *Naja haje* var. *capensis* Jan, 1863; *Naia flava* Boulenger, 1887; *Naja flava* Sternfeld, 1910

Ophidascaris naiae
Rhabdias fuscovenosa

Squamata

Family SCINCIDAE (Skinks)

GENUS *MABUYA*

1. *Mabuya quinquetaeniata* (Peters, 1854) (Rainbow skink)

Euprepes margaritifer Peters,1854; *Euprepes savignyi* Peters, 1854; *Euprepis gularis* Gray, 1864; *Euprepis kirkii* Gray, 1864; *Mabouia quinquetaeniata* de Jeude, 1895; *Mabouia margaritifer* Bocage, 1896; *Mabouia binotata* Bocage, 1896

Madathamugadia versterae
Spauligodon morgani
Spauligodon vojteki

2. *Mabuya striata* (Peters, 1844) (Striped skink)

Tropidolepisma striatum Peters, 1844; *Euprepes punctatissimus* A. Smith 1849; *Euprepes sundervallii* A. Smith 1849; *Euprepis granti* Gray, 1864; *Euprepes variegatus* Peters, 1869; *Euprepes wahlbergi* Peters, 1869; *Euprepes grutzneri* Peters, 1869; *Euprepes* (*Euprepis*) *striatus* Peters, 1882; *Mabuia wahlbergii* Boulenger, 1887; *Mabouia grutzneri* Boulenger, 1887; *Mabouia striata* Boulenger, 1887; *Mabuya striata* Parker, 1936

Skrjabinodon mabuiensis
Spauligodon morgani

3. *Mabuya sulcata sulcata* (Peters, 1862) (Western rock skink)

Euprepes olivaceus (*non* Gray) Peters, 1862; *Euprepes sulcatus* Peters, 1867; *Mabuya sulcata* Boulenger, 1887

Spauligodon petersi

4. *Mabuya varia varia* (Peters, 1867) (Variable skink)

Euprepes (*Euprepis*) *varius* Peters, 1867; *Euprepes olivierii* (*non* Dumeril & Bibron) A. Smith, 1849; *Euprepes olivieri* var. *albopunctatus* Bocage, 1869; *Euprepes* (*Mabuya*) *laevigatus* Peters, 1869; *Euprepes angolensis* Bocage, 1872; *Mabuya homalocephala* part., Boulenger, 1910; *Mabuya varia* Parker, 1936

Skrjabinodon mabuyae

Family LACERTIDAE (Old world lizards)

GENUS *ICHNOTROPIS*

1. *Ichnotropis squamulosa* Peters, 1854 (Common rough-scaled lizard)

Thubunaea fitzsimmonsi

Family GEKKONIDAE (Gekkos)

GENUS *HEMIDACTYLUS*

1. *Hemidactylus mabouia* (Moreau de Jonnes, 1818) (Moreau´s tropical house gecko)

Gecko mabouia Moreau de Jonnes, 1818; *Hemidactylus mercatorius* Gray 1831; *Hemidactylus gardineri* Boulenger, 1909; *Hemidactylus persimilis* Barbour & Loveridge, 1928; *Hemidactylus mandanus* Loveridge, 1936; *Hemidactylus platycephalus* Peters, 1854; *Hemidactylus mabouia* Dumeril & Bibron, 1836

Abbreviata polydentata
Physalopteroides asymmetrica
Skrjabinodon dossae
Spauligodon auziensis (?)
Spauligodon morgani

GENUS *PACHYDACTYLUS*

1. *Pachydactylus bibronii* A. Smith, 1846 (Bibron´s thick-toed gecko)

Pachydactylus bibronii A. Smith, 1846; *Homodactylus turneri* Gray, 1864; *Homodactylus bibronii* Gray, 1865; *Pachydactylus elegans* (*non* Gray) F. Müller, 1885; *Pachydactylus laevigatus* Fischer, 1888; *Pachydactylus bibronii laevigatus* Methuen & Hewitt, 1914

Spauligodon smithi

2. *Pachydactylus turneri* Gray, 1864 (Turner´s thick-toed gecko)

Pachydactylus bibronii A. Smith, 1846; *Homodactylus turneri* Gray, 1864; *Homodactylus bibronii* Gray, 1865; *Pachydactylus elegans* (*non* Gray) F. Müller, 1885; *Pachydactylus bibronii* A. Smith, 1846; *Pachydactylus laevigatus* Fischer, 1888; *Pachydactylus stellatus* Schmidt, 1933; *Pachydactylus bibronii turneri* Parker, 1936

Madathamugadia hiepei
Spauligodon timbavatiensis

Family AGAMIDAE (Agamas)

GENUS *ACANTHOSCERCUS*

1. *Acanthocerus atricollis* (A. Smith, 1849) (Southern tree agama)

Agama atricollis A. Smith, 1849; *Stellio capensis* A. Dumeril, 1851; *Stellio nigricollis* Bocage, 1866; *Stellio atricollis* Peters, 1881; *Agama gregorii* Gunther, 1894

Abbreviata nyassae
Strongyluris ornata

GENUS *AGAMA*

1. *Agama atra* Daudin, 1802 (Southern rock agama)

Agama atra Daudin, 1802; *Agama subspinosa* Gray, 1827; *Trapelus subhispidus* Kaup, 1827; *Phrynopis atra* Fitzinger, 1843; *Agama micropholis* Matschie, 1890; *Agama micropterolepis* Boulenger, 1896; *Agama holubi* Bocage, 1896

Parapharyngodon rotundatus
Physalopteroides impar impar
Strongyluris ornata

2a. *Agama aculeata aculeata*

Abbreviata sp.
Pharyngodon sp.

2b. *Agama aculeata distanti* Boulenger, 1902 (Ground agama)

Agama aculeata (*non* Merrem) Boettger, 1889; *Agama distanti* Boulenger, 1902;

Physalopteroides agamae

3. *Agama hispida armata* Peters, 1854 (Southern spiny agama)

Agama armata Peters, 1854, *Agama hispida mertensi* Wermuth, 1967; *Agama hispida distanti* (*non* Boulenger) Loveridge, 1923

Physalopteroides agamae
Skrjabinoptera wetzeli (?)

4. *Agama mossambica* Peters, 1854 (Mozambique agama)

Agama mossambica Peters, 1854; *Agama carniventris* Peters, 1874; *Agama colonorum* part. Loveridge, 1920

Thelandros alatus

Family CORDYLIDAE (Girdled lizards and their relatives)

GENUS *CORDYLUS*

1. *Cordylus cordylus* (Linnaeus 1758) (Cape girdled lizard)

Lacerta cordylus Linnaeus 1758; *Corylus verus* Laurenti, 1768; *Stellio cordylus* Daudin, 1802; *Cordylus griseus* Cuvier, 1829; *Corylus niger* Cuvier, 1829; *Cordylus dorsalis* Cuvier, 1829; *Zonorus vertebralis* Gray, 1838; *Zonorus cordylus* var. *niger* Rose, 1926; *Cordylus cordylus* Mertens, 1937

Physalopteroides impar impar

GENUS *PSEUDOCORDYLUS*

1. *Pseudocordylus microlepidotus* (Couvier, 1829) (Cape crag lizard)

Cordylus microlepidotus Couvier, 1829; *Zonurus microlepidotus* Gray,1831; *Zonurus wittii* Schlegel, 1834; *Cordylus* (*Pseudocordylus*) *montanus* and *melanotus* A. Smith, 1838; *Pseudocordylus montanus* Hewitt, 1927; *Pseudocordylus microlepidotus* Boulenger, 1885

Befilaria pseudocordyli
Madathamugadia ineichi
Parapharyngodon rotundatus

Family VARANIDAE (Monitor lizards)

GENUS *VARANUS*

1. *Varanus albigularis* (Daudin, 1802) (Rock monitor)

Tupinambis albigularis Daudin, 1802; *Monitor* (*Psammosaurus*) *albogularis* Gray, 1831; *Varanus gillii* A. Smith, 1831; *Varanus albogularis* Dumeril & Bibron, 1836; *Empagusia albogularis* Gray, 1838; *Monitor exanthematicus* var. *capensis* Schlegel, 1844; *Regenia albogularis* Gray, 1845; *Monitor albigularis* Peters, 1882; *Varanus exanthematicus albigularis* Schmidt, 1919

Abbreviata baylisi (?)
Orneoascaris schoutedeni
Tanqua tiara

2. *Varanus niloticus* Linnaeus, 1762 (Water monitor)

Lacerta nilotica Linnaeus, 1762; *Monitor saurus* Peters, 1882; *Varanus niloticus* Dumeril & Bibron, 1836

Abbreviata quadrovaria
Africana africana
Aplectana macintoshii
Hastospiculum macrophallos
Orneoascaris schoutedeni
Raillietascaris varani
Tanqua tiara

Family CHAMAELEONIDAE (Chameleons)

GENUS *CHAMAELEO*

1. *Chamaeleo dilepis* Leach, 1819 (Flap-neck chameleon)

Chamaeleo dilepis Leach, 1819; *Chamaeleon quilensis* Bocage, 1895; *Chamaeleon dilepis quilensis* Werner, 1902; *Chamaeleon parvilobus* Boulenger, 1887; *Chamaeleon dilepis parvilobus* Gunther, 1892

Abbreviata ortleppi ortleppi
Africana acuticeps
Hexametra applanata
Hexametra hexametra
Orneoascaris chrysanthemoides
Skrjabinoptera chamaeleontis
Strongyluris brevicaudata
Strongyluris elegans

2. *Chamaeleo namaquensis* A. Smith, 1831 (Namaqua chameleon)

Chamaeleo namaquensis A. Smith, 1831; *Chamaeleon namaquensis* Boulenger, 1887; *Chamaeleo tuberculiferus* Gray, 1845; *Phumanola namaquensis* Gray, 1864

Abbreviata damarensis

GENUS *BRADYPODION*

1. *Bradypodion pumila pumila* (Daudin, 1802) (Cape dwarf chameleon)

Chamaeleo pumilus Daudin, 1802; *Chamaeleon pumilus* Boulenger, 1887; *Chamaeleon margaritaeus* Merrem, 1820; *Bradypodium pumilus* Fitzinger, 1843; *Lophosaura pumila* Gray, 1864; *Chamaeleon ventralis* (*pro parte*) Werner, 1902; *Chamaeleon damaranus* (*pro parte*) Werner, 1902; *Microsaura pumila pumila* Fitzsimmons, 1943?

Strongyluris brevicaudata
Strongyluris capensis

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CHAPTER 2

Pentastomid parasites

of

reptiles

Onderstepoort Journal of Veterinary Research, 66:65–71 (1999)

Pentastomid infections in Nile crocodiles (*Crocodylus niloticus*) in the Kruger National Park, South Africa, with a description of the males of *Alofia simpsoni*

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ABSTRACT

JUNKER, KERSTIN, BOOMKER, J. & BOLTON, LORNA A. 1999. Pentastomid infections in the Nile crocodile (*Crocodylus niloticus*) in the Kruger National Park, South Africa, with a description of the males of *Alofia simpsoni*. *Onderstepoort Journal of Veterinary Research*, 66:65–71

Two Nile crocodiles were obtained from two different localities in the Kruger National Park, one a healthy specimen, the other in a severely debilitated condition. Both were males over 3 m long and both harboured the three pentastome genera *Sebekia*, *Alofia* and *Leiperia*. The genus *Sebekia* was represented by three species, *Sebekia wedli* Giglioli, 1922, *Sebekia cesarisi* Giglioli, 1922 and *Sebekia okavangoensis* Riley & Huchzermeyer, 1995. Of the genus *Alofia* two species, *Alofia simpsoni* Riley, 1994 and *Alofia nilotici* Riley & Huchzermeyer, 1995 were found. The male of *A. simpsoni*, formerly unknown, is described and the description of the females emended. *Leiperia cincinnalis* Sambon, 1922 was the only *Leiperia* present. Whereas *Sebekia* and *Alofia* were recovered from the bronchioles and lung parenchyma, female *Leiperia* occurred in the trachea and bronchi, and infective larvae as well as immature males and females, were collected from the lungs, the heart and the aorta. Adult *Subtriquetra* (Family Subtriquetridae) were not present in the nasopharynx of either crocodile. The intensity of infection was low in the healthy crocodile and had no negative effect on the host. In contrast, the debilitated crocodile was heavily infected and its poor condition is ascribed to its high pentastome burden. Histopathology revealed lesions in the tracheal wall and the lungs accompanied by chronic granulomata with secondary fungal infection as well as severe chronic multifocal granulomatous pneumonia.

Keywords: *Alofia*, *Crocodylus niloticus*, histopathology, *Leiperia*, pentastomes, *Sebekia*

INTRODUCTION

Pentastomes are endoparasites that mature in the respiratory tract of their final hosts, more than 90 % of which are reptilians, such as crocodiles, snakes and saurians (Baer 1952; Riley 1986). Of the existing eight families of pentastomes, two families, the Sebekidae and Subtriquetridae are known to infect crocodilians, using fish as intermediate hosts. The family Sebekidae comprises the genera *Sebekia* Sambon, 1922, *Alofia* Giglioli, 1922, *Selfia* Riley, 1994, *Leiperia* Sambon, 1922, *Agema* Riley, Hill & Huchzermeyer, 1997 and *Diesingia* Sambon, 1922. The first five genera, with the exception of a single species of *Sebekia*, which can reach maturity in freshwater chelonians (Dukes, Shealy & Rogers 1971), occur only in crocodilians while *Diesingia* has a chelonian definitive host (Overstreet, Self & Vliet 1985). The monogeneric family Subtriquetridae is exclusive to crocodilians (Riley, Spratt & Winch 1990).

The Nile crocodile, *Crocodylus niloticus*, is parasitised by three sebekiid genera, *Sebekia*, *Alofia* and *Leiperia* (Sambon 1922; Fain 1961). Most data were derived from studies conducted in Central Africa during the first part of this century and only recently have Riley & Huchzermeyer (1995) and Riley, Hill & Huchzermeyer (1997) studied new material.

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One of the *Alofia* species present in Africa, *Alofia simpsoni* Riley, 1994, has been described from only two females recovered from an unknown host in Ghana. In this article we add to the description of the females and describe the main characteristics of the males.

A fourth sebekiid genus present in Africa, *Agema*, has to date only been recorded from the slender-snouted crocodile, *Crocodylus cataphractus*, and the dwarf crocodile, *Osteolaemus tetraspis*, both of which occur in the equatorial rain forests of West and Central Africa (Riley *et al.* 1997). The only reports regarding pentastome infections in crocodilians in southern Africa are from a single Nile crocodile in Botswana (Riley & Huchzermeyer 1995) and two in the Kruger National Park, South Africa (Junker 1996; Junker, Boomker & Booyse 1998a, b).

In order to determine the pentastome fauna and their prevalence in crocodiles in the southern parts of Africa, a study on crocodile pentastomes was conducted in the Kruger National Park, South Africa during 1995 (Junker 1996). Some of the results of the unpublished thesis are presented in this paper.

MATERIALS AND METHODS

Hosts

Two Nile crocodiles were obtained from different localities in the Kruger National Park. Both specimens were male and measured 3,2 and 3,3 m in length, respectively. Crocodile A was caught in the Phabeni Dam (25°1'S, 31°15'E) in February 1995 with a baited cage-trap. It was immobilized with gallamine triethiodide (Flaxedil™) by means of an intra-muscular injection given with a pole dart. Subsequently the crocodile was transported to the laboratory at Skukuza where it was shot and examined immediately after death.

Crocodile B was in a severely debilitated condition and was shot at the Shimuwini Dam (23°42'S, 31°17'E) in June 1995. Its heart, lungs and trachea were placed in separate plastic bags filled with saline and kept cool. The organs were examined within 13 h of death. After removal of the trachea and the oesophagus, the nasopharynx, especially the area around the internal nostrils, was visually inspected for subtriquetrids.

Parasites

Pentastomes visible underneath the pleurae of the lungs were removed through an incision. Both lungs of each of the reptiles were opened along the bronchi and bronchioli with a pair of scissors and the parasites dissected out of the tissue. The hearts were opened with a pair of scissors, as well as the left and right aorta, and truncus pulmonalis.

All pentastome material was transferred into saline and used for experimental infections or fixed in 70% ethanol and mounted in Hoyer's medium for identification. Measurements were taken from whole mounted specimens according to the methods described by Riley *et al.* (1990).

The prevalence and intensity of pentastome infections were determined and the use of ecological terms is in accordance with the definitions given by Margolis, Esch, Holmes, Kuris & Schad (1982).

Pathology

Tissue samples of the trachea, lungs and heart were collected and fixed in 10% buffered formalin for histopathological examination. Tissue blocks were embedded in paraffin wax, sectioned at 5 mm and stained with eosin and haematoxylin. Fungi in the lung lesions were demonstrated by staining sections with Gomori's methenamine-silver nitrate (GMS) (Luna 1968) and the periodic acid-Schiff reaction (Pearse 1961).

RESULTS

Parasites

Both crocodiles harboured the three sebekiid genera *Leiperia*, *Sebekia* and *Alofia*. Female *Leiperia cincinnalis* occurred in the trachea and the bronchi, while *Sebekia* and *Alofia* were found in the bronchioles and the lung parenchyma. *Subtriquetra* was not found in the nasopharynx of either crocodile.

Fifteen adult pentastomes and 14 nymphs were obtained from Crocodile A. *Sebekia okavangoensis* was the dominant species with nine adult specimens being present. A single *S. okavangoensis* male was found in the aorta, the remainder being in the bronchioles. One *Sebekia wedli* male was collected from the lungs, as well as a single *Sebekia cesarisi* female and one male *Alofia nilotici*. All adult pentastomes were sexually mature specimens as indicated by the fully developed copulatory spicules of the males and the presence of eggs in the uteri of the females. Also present in the lungs were 11 infective sebekiid larvae other than *Leiperia*. Three infective larvae of *L. cincinnalis* were attached to the aorta, while three adult females were collected from the trachea.

Crocodile B was heavily parasitised and harboured six different pentastome species. A total of 177 adults and 62 infective larvae were recovered of which *S. wedli* from the lungs ($n=75$) accounted for nearly half of the adult collection. A single *S. cesarisi* female and seven males, one male and two female *S. okavangoensis* and six adult *Sebekia* spp. females that could not be identified to the species level were present in the lungs. Four infective larvae were recovered from the same site. The genus *Alofia* was represented by 61 *A. simpsoni* together with one male and one female *A. nilotici*. A single infective *Alofia* sp. larva (ascribed to this genus because of the characteristically U-shaped oral cadre) occurred in the heart. The sex ratio was in favour of females, it being 91 % in *S. wedli* and 79 % in *A. simpsoni*.

Fifteen patent *L. cincinnalis* females were obtained from Crocodile B. Two were attached to the tracheal wall and three were recovered from the right bronchus. The remaining *Leiperia* females were lumped together in a mucous matrix in the left bronchus, severely obstructing the airflow. Males were not present. Infective *L. cincinnalis* larvae ($n = 57$) were collected from both lungs, the heart and from two big clusters in the pulmonary artery. The latter larvae were embedded in a mucous matrix that partially obstructed the lumen of the vessel. Also isolated from the clusters were seven specimens that carried simple hooks and retained the old cuticle of the infective larval stages. One immature male and an immature female were identified while the sex of the other five specimens remains undetermined.

Additions to the description of *Alofia simpsoni* Riley, 1994

FEMALES ($n = 12$)

The body-shape is dominated by the bulbous caudal extremity. The body length is 29 ± 1,6 mm and the maximum width is 2,0 ± 0,2 mm. The oral cadre is 318,2 ± 27,3 µm long and 151,3 ± 16,4 µm wide, with an overall length of 366,7 ± 32,2 µm. Hooks are 124,6 ± 8,5 µm long and the fulcra measure 274,5 ± 30,9 µm. Annuli number 82 ± 2.

MALES ($n = 13$)

Males of *A. simpsoni* are markedly smaller than the females and lack the bulbous tail. The body length averages 8,7 ± 0,9 mm and it is 1,1 ± 0,2 mm wide. The smooth hooks are long (104,4 ± 3,5 µm) and slender, bent almost through a right angle and are devoid of spines (Fig. 1A, B). The fulcra measure 230,1 ± 15,2 µm. The oral cadre is U-shaped, possesses a small peg-like extension into the pharynx, and is 207,2 ± 15,7 µm long and 104,1 ± 5,0 µm wide (Fig. 1A, C). It has an overall length of 267,6 ± 16,9 mm. The copulatory spicules are typically alofian in that the smooth-surfaced shorter extension of the base of the cowry-shell ends in a double hooked collar. The second projection is elongated and its surface marked by transverse grooves (Fig. 1A, D, E). The length of the cowry-shell, including the short extension, averages 300,4 ± 14,3 µm and the total length, including the longer extension, is 372,8 ± 30,5 µm. The opening in the cowry-shell is shaped like a long ellipse. The number of annuli varies from 79–83.

Pathology

Crocodile A was in good condition and the lungs and heart were not impaired in their functionality. The attachment sites of pentastomes in the lungs and trachea were characterized by an area of mild coagulative necrosis with eosinophilic and heterophilic infiltrates, with associated oedema and haemorrhage in the surrounding tissue. Migration tracts were seen as multifocal thin-walled cavities lined by scattered multinucleated giant cells and containing coagulated blood and haematoidin. A pentastome was present in the aorta lumen, attached to the endothelium. At the attachment site focal erosion of the endothelium, associated oedema, haemorrhage and infiltration of small numbers of macrophages and lymphocytes were seen.

Crocodile B was severely emaciated. It only weighed between 105 and 110 kg whereas the average normal weight of a crocodile of 3,3 m is around 155 kg (Loveridge & Blake 1972). Macroscopically part of the bronchi and pulmonary aorta were obstructed by females and infective larvae of *L. cincinnalis*, respectively. The outer surface of the trachea was covered by numerous brown nodules, which represented migration tracts and attachment sites of the pentastomes. Their histopathological appearance was as described for Crocodile A. The anterior part of a female embedded in the tracheal mucosa and attached to the wall of the trachea is illustrated in Fig. 2A. A chronic multifocal granulomatous pneumonia associated with many intralesional pentastome adults, larvae and eggs (Fig. 2B) was present. Several of the lesions in the trachea and lung were enlarged, containing abundant eosinophilic necrotic debris surrounded by multinucleated giant cells. Associated with some of these lesions were a myriad of fungal hyphae, 3–6 µm diameter, regularly septate with random branches at 90° angles. One such a fungal lesion is illustrated in Fig. 2C. Alternatively, these lesions contained many bacterial colonies within the necrotic centres. The hooks of the pentastomes attached to the pulmonary arterial wall elicited a moderate chronic multifocal granulomatous arteritis.

DISCUSSION

Parasites

The pentastomid fauna of *C. niloticus* is characterized by a high diversity. Three different genera of pentastomes were recovered from both the crocodiles examined and a total of six sebekiid species were present. Although adults of *Subtriquetra* were not recovered from either of the crocodiles, the presence of infective larvae of *Subtriquetra rileyi* in two cichlid fish species in the Kruger National Park indicates that Nile crocodiles probably also serve as hosts for this pentastome (Junker *et al.* 1998a). *A.*

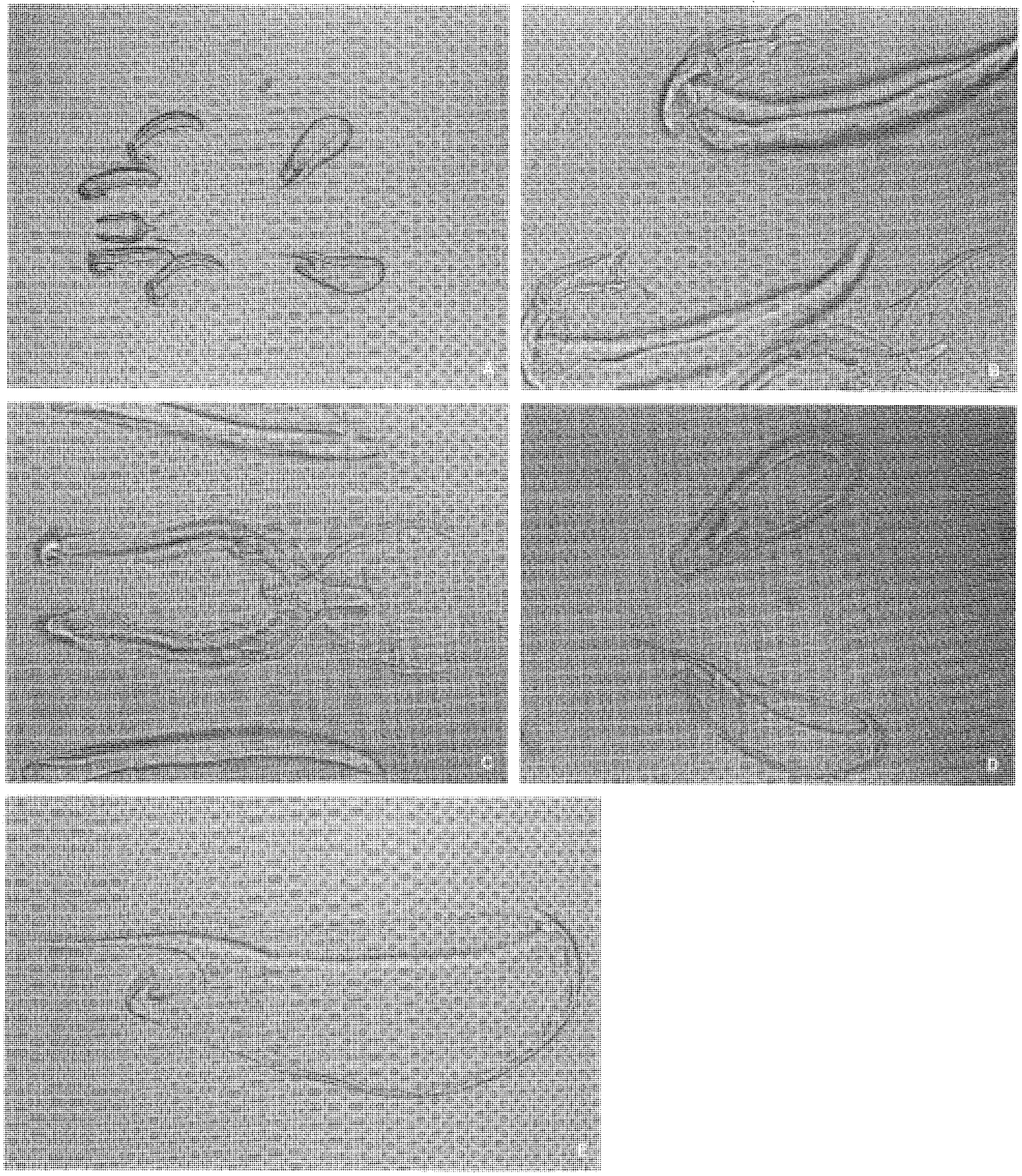

FIG. 1 *Alofia simpsoni*

- A Cephalothorax of a male, depicting the alignment of the hooks, the oral cadre and the copulatory spicules
- B Detail of the left posterior and anterior hook of a male. The hooks are smooth and bent at almost a right angle
- C U-shaped oral cadre of a male showing the peg-like extension into the oesophagus
- D Right and left copulatory spicule, in lateral and ventral view, respectively. Note the double hooked collar of the shorter extension of the cowry-shell
- E Detail of right copulatory spicule seen in A. The long, spatulate extension of the cowry-shell is marked by chitinized ridges. In the right upper corner parts of the coiled cirrus are visible

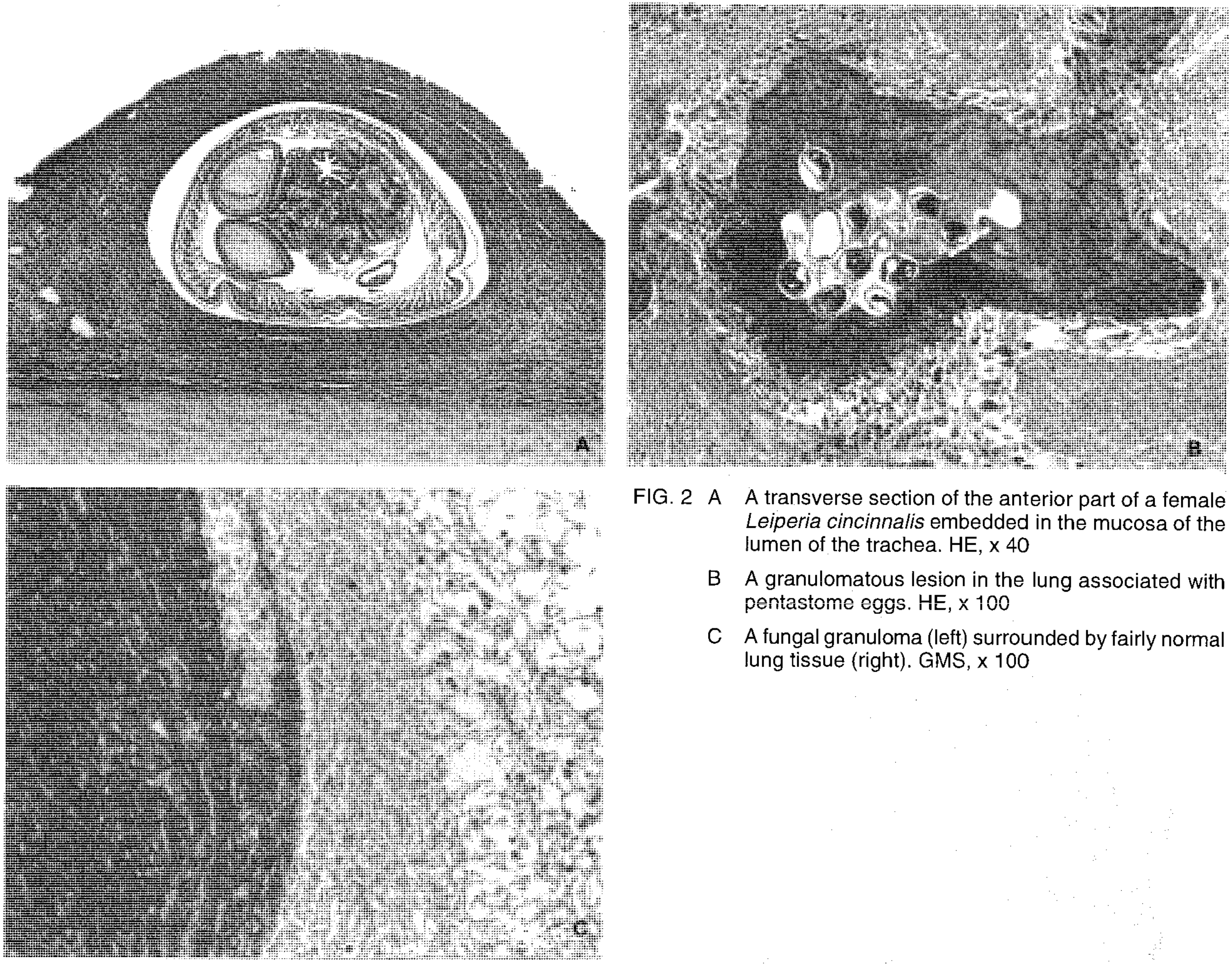

FIG. 2 A A transverse section of the anterior part of a female *Leiperia cincinnalis* embedded in the mucosa of the lumen of the trachea. HE, x 40

B A granulomatous lesion in the lung associated with pentastome eggs. HE, x 100

C A fungal granuloma (left) surrounded by fairly normal lung tissue (right). GMS, x 100

simpsoni has thus far only been recorded from an unknown host, probably a crocodilian (Riley 1994), and its presence in Nile crocodiles constitutes a new host record for the parasite.

As opposed to snakes in which multiple infections seldom occur (Fain 1961), multiple infections in crocodilians are common. Riley & Huchzermeyer (1995) found four different pentastome species in a single Nile crocodile from Botswana. Similarly, the Indo-pacific crocodile, *Crocodylus porosus*, is known to be the final host of seven species representing four genera (Riley 1994).

Most pentastomes were encountered at attachment sites considered typical for the genus and its developmental stages. Thus, infective larvae of *L. cincinnalis* were in the heart and aorta from where they invade the trachea and bronchi (Rodhain & Vuylsteke 1932; Heymons 1939).

The occurrence of a *S. okavangoensis* male in the aorta of Crocodile A and an infective larva of *A. simpsoni* in that of Crocodile B is unusual, since these sebekiids occur in the bronchioli and lung parenchyma (Fain 1961; Riley 1994). Adult pentastomes start migrating from the lung tissue following the death of the host (Overstreet *et al.* 1985) which is ascribed to declining oxygen levels (Riley & Huchzermeyer 1995). Crocodile A was necropsied immediately following its death but the muscle relaxant may have impaired its breathing. We therefore assume that the parasite's presence was due to post-mortal migration. Due to the long interval before the organs of Crocodile B were processed, we make the same assumption for *A. simpsoni*.

Some authors have observed that in spite of a balanced sex ratio in the infective larvae, the sex ratio in mature infections shifts in favour of the females (Leuckart 1860; Hett 1924; Riley 1972). Based on observations of the genera *Kiricephalus* and *Waddycephalus*, Riley & Self (1980; 1981) conclude that this is due to the comparatively shorter life span of pentastome males. Our findings, especially concerning *S. wedli* and *A. simpsoni*, support this.

Few data exist as regards the prevalence and intensity of pentastomid infections in the Nile crocodile.

The Phabeni Dam in the south-west and the Shimuwini Dam in the north-west of the Park are part of two unrelated river systems, the Sabie River/ Phabeni River in the south and the Letaba River in the north. The recovery of pentastomes in each of the Nile crocodiles indicates that the parasites are widespread in the Park and not limited to a single river system.

Apart from this study, only Riley & Huchzermeyer (1995) provide the intensity of pentastome infection of a single Nile crocodile in Botswana. This reptile harboured 94 adult pentastomids. Almost as little is known about the slender-snouted crocodile and the dwarf crocodile. Riley *et al.* (1997) collected eight pentastomids from a juvenile *C. cataphractus* from the Congo Republic. At the same occasion, pentastomes from 15 specimens of *O. tetraspis* were recovered. The prevalence of infection was 80 % with a mean intensity of 24 (Riley *et al.* 1997). More detailed information is available for North American alligators. Seven alligators from Georgia were infected with 30–40 pentastomids each (Deakins 1971), and 93 % of 30 alligators examined by Cherry & Ager (1982) had 10,6 (1–77) adults. The intensity of infection in the two crocodiles examined during this study differed considerably. While Crocodile A carried a light pentastome burden (15 adults), Crocodile B was heavily infected, and the recovery of 177 adults exceeds the intensities formerly recorded for crocodilians by far.

Alofia simpsoni Riley, 1994

The main characteristics of the females of *A. simpsoni* described in this paper fit in well with Riley's (1994) description. The overall length of the oral cadre was given as 355 µm, but according to Riley (1994) it was not possible to measure any other dimensions of the buccal complex due to the way in which the specimens were mounted.

There is a notable difference in our annulus counts when compared to that given by Riley (1994). We are not able to explain the discrepancy, but considering the number of specimens at our disposal we believe our counts to be representative.

The males of *A. simpsoni* are distinctly different from *A. nilotici*, in that the hooks of *A. simpsoni* are smooth whereas those of *A. nilotici* are equipped with a patch of minute spines. The copulatory spicules of *A. simpsoni* are markedly smaller than those of *A. nilotici* (372,8 µm long as opposed to 585 and 520 µm, respectively).

Pathology

Ladds & Sims (1990) necropsied 54 young crocodiles, *C. porosus* and *C. novaeguineae*, eight of which were infected with pentastomes. The same histopathological picture was evident in our crocodiles. In three of the cases, the infection with pentastomes was considered one of the main reasons for the poor condition of these animals (Ladds & Sims 1990). The presence of granulomata in the lungs and trachea of Crocodile B were often associated with bacterial colonies or fungal infiltration, which conforms to the findings of Deakins (1971). The damage caused to the lung epithelium by pentastomes often gives way to secondary infections (Deakins 1971). In alligators, *Sebekia* spp. facilitate infection with *Aeromonas* sp. (Shotts, Gaines, Martin & Prestwood 1972; Hazen, Aho, Murphy, Esch & Schmidt 1978).

The mild pentastome infection in Crocodile A had no apparent adverse effect, indicating that, under natural conditions, Nile crocodiles are able to tolerate pentastome infections. Boyce, Cardheilac, Lane, Buergelt & King (1984) came to the same conclusion when studying sebekiosis in alligators. The distinct clinical signs seen in Crocodile B, however, emphasize that given the right circumstances, pentastomids can have a serious impact on the host. We ascribe the poor condition of Crocodile B to the heavy infection, the pentastome activity causing extensive damage to the lungs and heart of the host. During post mortem examination no injuries accounting for Crocodile B's condition were found. A possible explanation for the large number of pentastomes may be found in the environmental circumstances at the Shimuwini Dam during the months prior to our studies: a large number of crocodiles congregated in front of the dam wall, feeding extensively on fish that got trapped against this structure.

Unfortunately, the prevalence and intensity of infection in fish at the Shimuwini Dam could not be established. However, infection rates in Mozambique bream, *Oreochromis mossambicus*, and red-breasted bream, *Tilapia rendalli*, from the Phabeni Dam were low (Junker *et al.* 1998a). This suggests that the high density of intermediate hosts and thus the high intake of fish by the final hosts, even though the infection rate in the fish might have been low, exposed the crocodiles to a concentration of infective pentastomid larvae that would otherwise not be encountered. These are important considerations as regard the conservation of the Nile crocodile. It illustrates that under certain conditions, pentastomes can pose a serious threat to their definitive hosts. Environmental destruction and decreasing water levels due to human activity imply that crocodiles are restricted to a decreasing number of suitable habitats. The resulting increase in population density may enhance the spreading of parasitic infections drastically.

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Leiperia cincinnalis Sambon, 1922 (Pentastomida) from Nile crocodiles *Crocodylus niloticus* in the Kruger National Park, South Africa, with a description of the male

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Abstract

A single male and several adult females of the pentastomid *Leiperia cincinnalis* were recovered from the trachea of five of six Nile crocodiles examined in 1995 and 1998. Infective larvae, pre-adult males and females, as well as mature males, occurred in clusters in the pulmonary artery but infective larvae and pre-adult females were also occasionally taken from the lungs. Irrespective of the developmental stage, the intensity of infection was 3, 6, 48, 72 and 79. Sixty-four percent of eggs recovered from the posterior part of the uterus of a patent *L. cincinnalis* female contained fully-developed primary larvae and these were used to infect 24 Mozambique bream *Oreochromis mossambicus*. Within a week of infection all the fish died and hatched primary larvae were recovered from the stomach and anterior part of the intestine. Eggs that had not hatched were found to be unsegmented. The total primary larval count in seven fish was 18, 12, 1, 25, 16, >40 and >50. Descriptions with detailed measurements are given of the females, the males, the eggs, the primary larvae and the infective larvae of *L. cincinnalis*.

Introduction

Leiperia cincinnalis Sambon, 1922 (syn. *Reighardia cincinnalis* Vaney & Sambon, 1910) (Pentastomida) is common in Nile crocodiles *Crocodylus niloticus* Laurenti on the African continent (Sambon, 1922; Heymons, 1940; Fain, 1961; Junker, 1996). Although known for a long time, little information was available on the life-cycle of *L. cincinnalis* and the descriptions given were often inadequate. Riley & Huchzermeyer (1996) re-assessed the genus *Leiperia* Sambon, 1922 and re-examined material of *L. cincinnalis* collected by various authors. None of the collections included mature males, but the morphology of the females, nymphs and pre-adults were described in considerable detail (Riley & Huchzermeyer, 1996).

In 1995 and 1998 experimental and field studies were conducted on pentastome infections of fish and crocodiles in the Kruger National Park (KNP) in South Africa (Junker, 1996; Junker, Boomker & Booyse, 1998a,b). Although the pentastome genera *Alofia* Giglioli, 1922 and *Sebekia* Sambon, 1922 were recovered from the crocodiles, in this paper we describe our findings and present additional data on the measurements and morphology of the females and the infective larvae of *L. cincinnalis*. The eggs and primary larvae are also described, and observations on the life-cycle are provided. The morphology of the males of *L. cincinnalis* is described for the first time.

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Table 1. Collection data of Nile crocodiles from the Kruger National Park.

Host number	Date collected	Locality	Sex	Length (m)	Condition
A/95	22/2/95	Phabeni Dam (25°1′ S, 31°15′ E)	M	3.2	good
B/95	27/6/95	Shimuwini Dam (23°42′ S, 31°17′ E)	M	3.3	emaciated
1/98	10/6/98	Silwervis Dam (23°13′ S, 30°12′ E)	F	2.8	good
2/98	10/6/98	Silwervis Dam (23°13′ S, 30°12′ E)	M	2.4	good
3/98	10/6/98	Silwervis Dam (23°13′ S, 30°12′ E)	F	3.2	good
4/98	10/6/98	Silwervis Dam (23°13′ S, 30°12′ E)	F	2.7	good

F, Female; M, Male.

Materials and methods

The collection data of the crocodiles examined are listed in Table 1. The crocodiles from the Phabeni and Silwervis Dams were caught in a baited cage and immobilised with gallamine triethiodide (Flaxedil$^{\mathrm{TM}}$) before they were shot. The specimen from the Shimuwini Dam was killed with a single shot through the brain.

The nasopharynx, trachea, lungs, heart and aorta of each crocodile were examined. After removal of the trachea and the oesophagus, the nasopharynx, especially the area just above the internal nostrils, was visually checked for pentastomids belonging to the genus *Subtriquetra* Sambon, 1922. The trachea was opened lengthwise and all *Leiperia* removed. The lungs were cut open along the bronchi and bronchioles using a pair of scissors and placed into trays containing phosphate buffered saline (PBS). Pentastomes were either removed directly from the lung tissue or collected from the PBS after migrating out of the lungs.

The heart and its blood vessels were cut open and the chambers and inner surface of the blood vessels examined.

For morphological studies pentastomes were fixed and stored in cold 70% ethyl alcohol, and later mounted and cleared in Hoyer's medium. Those pentastomes used for infection of the intermediate fish hosts were kept in PBS.

Twenty-four Mozambique bream *Oreochromis mossambicus* Peters (50–70 mm long, obtained from a local breeder) were infected with eggs of *L. cincinnalis* from the crocodile from the Phabeni Dam. Eggs were collected from the posterior part of the uterus and concentrated in regular tap-water. In order to check the viability of the eggs, a drop of the egg-suspension was heated to 30°C and the number of hatched larvae was estimated.

Groups of four bream each were placed into one-litre beakers supplied with air stones and filled with 600 ml of water. To each beaker a drop of the egg-suspension was added. The fish were infected overnight and all died after 6–8 d. Within a few hours of death the abdominal cavity of each fish was opened by ventral incision and rinsed over a 38 μm sieve. The stomach, intestine and swim-bladder of each were placed between two perspex slides exerting light pressure. These, as well as the residue on the sieve, were examined under a stereoscopic microscope.

Results

Leiperia cincinnalis is a common pentastome in the Nile crocodile and five of six crocodiles examined in this study harboured this parasite (Table 2 summarises the numbers and developmental stages recovered from the respective hosts).

Three adult *L. cincinnalis* females were attached to the trachea and three infective larvae recovered from the pulmonary artery of Crocodile A/95 while Crocodile B/95 harboured 15 patent females in the trachea and bronchi. A total of 64 immature instars were recovered from the lungs, the heart and mainly the aorta pulmonalis, where the immatures occurred in two clusters.

A single infective larva of *L. cincinnalis* was found in the lungs of Crocodile 1/98, and a cluster of 47 specimens, representing different developmental stages together with cast cuticles, were recovered from the aorta pulmonalis. Six of the *Leiperia* were fully-developed males. In two other specimens well sclerotised cirrus tips were visible, but the single hooks, the oral cadre and the copulatory spicules were hardly chitinised. Eleven of the parasites were infective nymphs carrying double hooks. Many of the specimens with

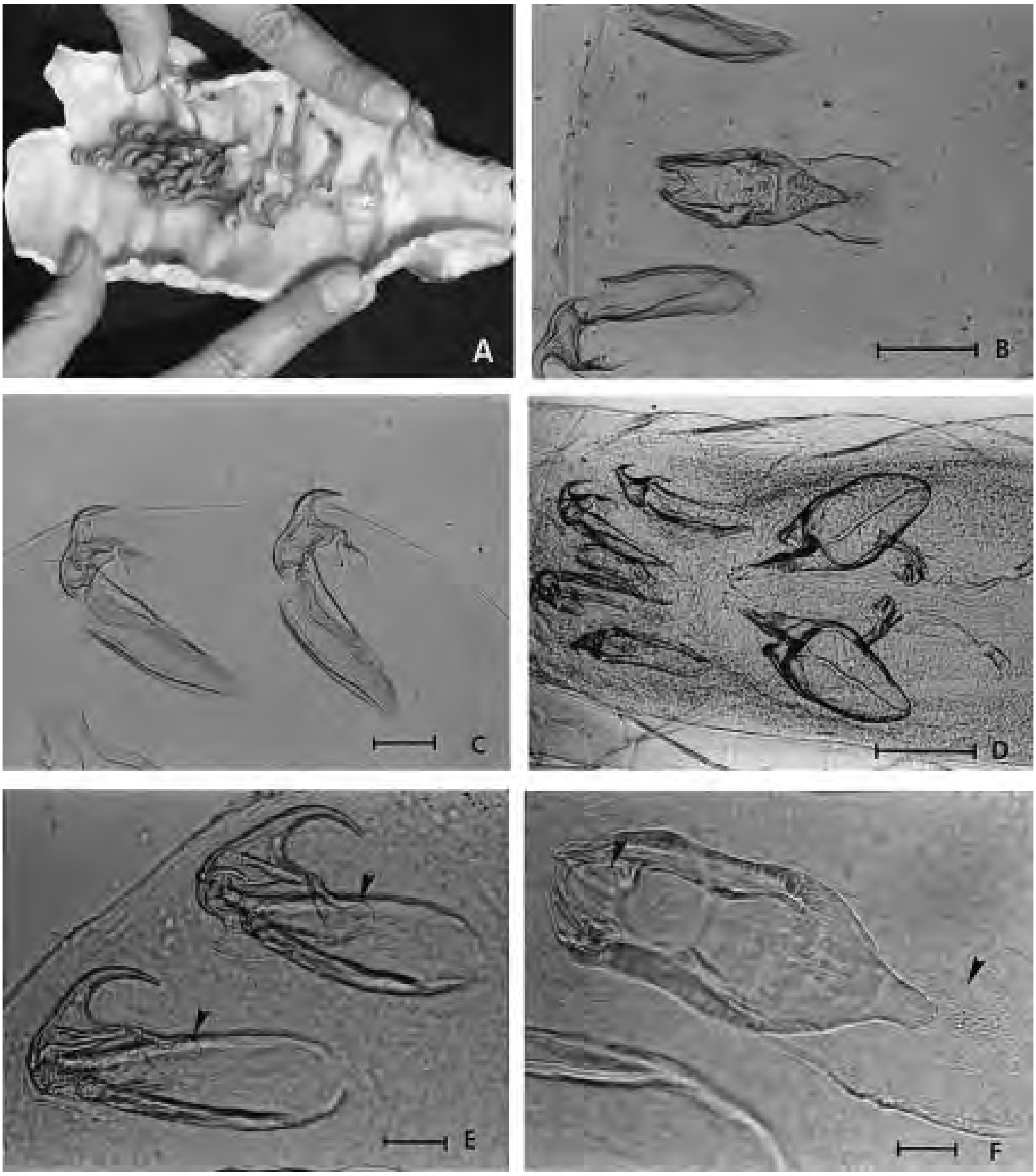

Figure 1. A. Mature females attached to a bronchus of the crocodile from the Shimuwini Dam, Kruger National Park. B. The right anterior hook and oral cadre of a mature female recovered from the same crocodile. The hook carries a distinct dorsal notch. C. Detail of the left hooks of another mature female from the Shimuwini crocodile, possessing a prominent dorsal notch. D. The anterior part of a male (No. 4.18/98) showing the hooks, the oral cadre and the copulatory spicules. The elaborate cirrus tips as well as the chitinised armoured tubes that form part of the cirri are visible furthest right. E. Detail of the left posterior and anterior hook of the male recovered from the trachea (No. 2.3/98). The hooks are flat-topped with only a slight indent in the dorsal margin. The anterior apodemes are lobe-like and permeated by pores (arrows). F. Oral cadre of specimen No. 2.3/98 showing the numerous pores around the pharynx as well as the large anterior flanges (arrows). *Scale-bars*: B,D, 400 μm; C, 200 μm; E, 100 μm; F, 50 μm.

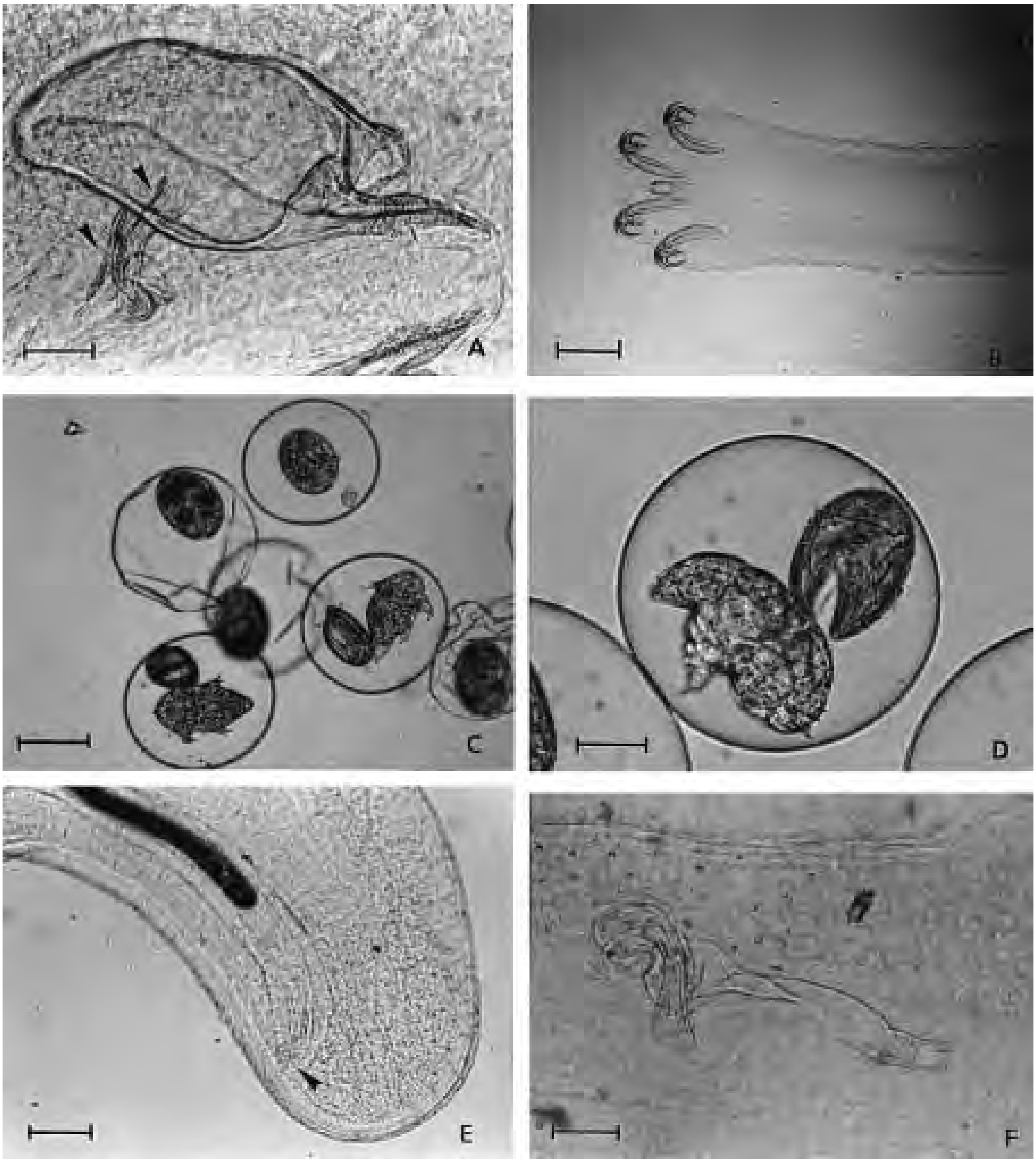

Figure 2. A. Right copulatory spicule (No. 4.19/98). The collar around the spatulate extension is heavily chitinised and carries rings of chitin. The cirrus tip is flared (upper arrow) and accompanied by a strongly-chitinised scoop-like structure (lower arrow). B. The anterior part of an infective larva, showing the large double-hooks and the comparatively small oral cadre. C. Eggs of *L. cincinnalis* and two hatching primary larvae. D. Detail of a primary larva and split inner egg membrane. E. Posterior end of female (No. 2.1/98) found *in copula* showing the eversed vaginal lips (arrow). Part of the ruptured cirrus, visible as a transparent thread (left), is next to the abdomen. F. Cirrus tip of the male located in the vagina of No.2.1/98. Note the prominent chloride cell pore caps on the cuticula of the female. *Scale-bars*: A,C,F, 100 μm; B,E, 500 μm; D, 50 μm.

Table 2. The numbers and developmental stages of *Leiperia cincinnalis* recovered from Nile crocodiles in the Kruger National Park.

Host number	Developmental stage				Total
	Females	Males	Pre-adults	Infective larvae	
A/95	3	0	0	3	6
B/95	15	0	7	57	79
1/98	0	6	30	12	48
2/98	2	1	0	0	3
3/98	0	0	0	0	0
4/98	7	10	22	33	72

simple hooks were still surrounded by the old cuticula of the infective larva.

Crocodile 2/98 harboured two female *L. cincinnalis* in the trachea and a single male was found attached next to one of the females. The cirrus tips were absent and the anterior part of the spatulate extension of both the copulatory spicules projected through the anterior genital opening. One of the cirrus tips was seen in the anterior third of the vagina of female No. 2.1/98 (Figure 2F) and the vaginal lips of the latter specimen were still everted (Figure 2E). The female was 4.5 cm long and 1 mm wide, and the abdomen was only just beginning to coil. No *Leiperia* were found in the pulmonary artery or the lungs.

No *L. cincinnalis* were recovered from Crocodile 3/98, but Crocodile 4/98 harboured 72 specimens. Eleven females, ranging in body length from 4.5 to 10.5 cm, were attached to the trachea and the uteri of four, all of them less than 6 cm long, contained no eggs, but the latter were present in the remainder. Two prepatent *Leiperia* females were found in the lungs but were damaged in the recovery process. The remaining 59 specimens were collected from the pulmonary artery, where they formed a cluster similar to that found in Crocodile 1/98. A total of 15 males were isolated from this cluster; 10 of these were fully mature, but in the remainder the copulatory spicules were not yet fully developed. One of the mature males was still within the cuticula of the infective larva and the simple hooks of another preceding instar were visible. The sex of another 11 *L. cincinnalis*, with simple hooks, remained undetermined. In addition, 33 infective larvae were present.

Six days after the experimental infection, two *O. mossambicus* were found dead and during the following two days all the fish died. Upon dissection, empty egg shells or the primary larvae themselves were found in the stomach and anterior part of the intestine. We also recovered intact pentastomid eggs, the majority of which were unsegmented. The primary larval count in seven fish was 18, 12, 1, 25, 16, >40 and >50.

Leiperia cincinnalis **Sambon, 1922**

Description

Females (Table 3)

The general morphology of the females of *L. cincinnalis* examined in this study conformed largely to that described by Riley & Huchzermeyer (1996). Additional and comparative data are presented in Table 3.

Every fully-mature, gravid female examined (n = 6) possessed hooks with a prominent dorsal notch (Figure 1B,C). Two females recovered from the trachea (No. 2.1/98 and No. 4.7/98, 5.5 cm long) had hooks marked by only a slight indentation in the dorsal surface. These specimens were considerably shorter and had not reached patency. The hooks, as well as measurements of the oral cadre of one specimen (No. 4.7/98), were slightly smaller than those of the patent females. An immature female from the aorta pulmonalis carried flat-topped hooks, while those of another specimen (No. 2.1/98) could not be measured.

Males (Table 4)

Well-fixed male specimens possessed a straight, cylindrical abdomen, tapering slightly to a rounded end. The male recovered from the trachea was 2.0 cm long while the body length of 3 males taken from the aorta ranged from 1.8 to 2.0 cm.

Heavily chitinised fulcra supported the prominent hooks (Figure 1E). In comparison to the length of the hooks, the fulcra appeared rather broad and compact.

Table 3. The main characteristics of female *Leiperia cincinnalis* recovered from Nile crocodiles in the Kruger National Park in 1995 and 1998. For comparative purposes data of Riley & Huchzermeyer (1996) and Junker (1996) are included. All measurements are in micrometres unless otherwise indicated.

Source	Specimen number	Number of annuli	Body length (mm)	Mouth dimensions			Hook dimensions			
				Overall length	Cadre length	Width	Hook length	Base length	Hook depth	Fulcrum length
This paper	4.1/98	NM	105	920	727	285	NM	NM	NM	NM
	4.3/98	NM	100	925	750	322	313	259	NM	NM
	4.7/98[a]	NM	55	690	552	212	262	203	86	528
	4.9/98	NM	95	NM	NM	NM	353	267	94	644
	2.1/95	NM	NM	925	736	308	NM	NM	NM	NM
	2.2/95	NM	NM	925	745	281	NM	NM	NM	NM
Junker (1996)	CWT2	NM	131	NM	NM	NM	354	NM	NM	645
	CWT3	100	110	824	689	275	348	NM	NM	651
	Lei3	100	120	915	750	NM	355	NM	NM	703
Riley & Huchzermeyer (1996)	1947.12.1.57-59	NM	NM	NM	NM	NM	480	220	NM	810
	1927.11.15.28-30	NM	NM	NM	NM	NM	463	218	NM	705
	1932.7.22.1	NM	85?	1020	850	375	400	180	NM	640

[a] Uterus devoid of eggs.

NM, Not measured.

The term "base length" in this paper refers to the same structure as the term "hook depth" used by Riley & Huchzermeyer (1996).

Table 4. The main characteristics of the males of *Leiperia cincinnalis* recovered from Nile crocodiles in the Kruger National Park. All specimens were recovered from the pulmonary artery (AP), excepting 2.3/98 from the trachea of Crocodile 2/98. For comparative purposes data of three immature males (1927.III.10-6-11) examined by Riley & Huchzermeyer (1996) are included. All measurements are in micrometres.

Specimen number	Mouth dimensions			Hook dimensions				Copulatory spicules				
	Overall length	Cadre length	Width	Hook length	Base length	Hook depth	Fulcrum length	Total length	Cowry shell length	Width	Length of armoured tube	Number of grooves
4.18/98	432	340	106	194b	150b	90b	420b	782	607	NM	104	14
4.19/98	405	306	120	NM	NM	NM	NM	757	612	NM	113	13
4.20/98	426	338	113	232a	166a	87a	437a	782	605	207a	108	14a
4.21/98	474	363	113	232a	163a	90a	426b	814	637	NM	115a	11
4.22/98	465	366	NM	240b	166b	78b	447b	817	621	202a	124a	13
4.23/98	460	343	124	216a	161a	NM	431c	780	614	NM	115a	13
4.24/98	458	336	129	196b	153b	NM	411	821	623	NM	127	12
4.25/98	451	331	120	189a	145a	NM	423c	819	621	NM	133a	13
4.26/98	449	343	133	NM	NM	NM	432b	803	616	NM	120	14
4.27/98	446	331	120	244b	174b	NM	407a	798	623	NM	133a	16
1.16/98	426	317	104	NM	NM	NM	428b	NM	637	NM	110a	NM
1.17/98	NM	NM	NM	216a	152a	90a	NM	791a	607	NM	104	NM
1.18/98	NM	NM	NM	255a	182a	90a	437a	805a	649a	NM	NM	NM
1.19/98	462	340	110	245c	171c	87c	NM	837	637	NM	108	14
1.20/98	497	386	115	206b	158b	93b	NM	787a	616a	NM	101a	NM
1.6/98	492	386	136	245c	169c	82c	453a	844	628	NM	129	12
Average (AP)	453	345	119	224	162	87	429	802	622	205	116	13
SD (AP)	26	23	10	23	11	5	14	24	13	NM3	11	1
2.3/98	405	320	127	273	170c	81c	NM	780	614	NM	NM	13a
1927.III.10-6.11d	NM	NM	NM	290	NM	115	645	NM	NM	NM	NM	NM
	NM	NM	NM	280	NM	120	600	NM	NM	NM	NM	NM
	430	280	125	NM	NM	120	580	NM	NM	NM	NM	NM

[a] Only one feature was measured.
[b] Only two features were measured.
[c] Only three features were measured.
[d] After Riley & Huchzermeyer (1996).

The anterior apodeme of the hooks widened into a lobe-like structure permeated by numerous pores (Figure 1E). A certain degree of variability characterised the hook morphology of male *L. cincinnalis* (n = 17). In some specimens the hooks were flat-topped, in others only slight depressions were visible and in yet others, hooks had a distinct dorsal notch. Flat-topped hooks and hooks with a dorsal notch could at times be seen in the same specimen. The hooks and fulcra of the males were considerably shorter than those of the females and the measurements were actually nearer to those of the infective larvae (Junker, 1996). However, their gross morphology closely resembled that of females. This was true of the oral cadre with its characteristic *Leiperia* shape (Figure 1F). Starting in the posterior third of the oral cadre, the lateral prongs of the oral cadre merged gradually, giving it a V-shaped profile (Riley & Huchzermeyer, 1996). Both the large anterior flanges, as well as the area between the sclerotized supports of the pharynx, possessed the same pores as females (Riley & Huchzermeyer, 1996) (Figure 1B,F).

The paired copulatory spicules were strongly chitinised and the spatulate anterior extension carried an average of 13 rings of chitin folds while the collar around the neck of the latter extension was marked by heavy chitinous rugosities (Figures 1D, 2A, 3A,B). The cirrus tip was “a flattened trumpet of longitudinally-striated chitin” (Riley & Huchzermeyer, 1996) (Figures 2A, 3A,C) and the whole structure was demarcated from the remaining unmodified section of the cirrus by “a short armoured tube supported by rings of chitin”, as described for *Leiperia australiensis* Riley & Huchzermeyer, 1996 by the latter authors. Parallel to the trumpet, and in close association, a second chitinous structure was visible (Figures 2A, 3C). This structure gave the impression of a scoop with serrated sides rolled up towards the mid-line. It was very similar in shape to the gubernaculum of *Sambonia lohrmanni* (Sambon 1910) Noc & Giglioli, 1922 (see Fain, 1961). While often separated under cover-slip pressure, in some specimens the trumpet ran through the scoop and the latter served as a support.

Infective larvae (Table 5)

The distinctly elongate and slender body, together with the rounded shape of the head, gave the infective larvae of *L. cincinnalis* a characteristic appearance, which sets it apart from other sebekiid larvae (Junker et al., 1998a). As detailed descriptions of the morphology of the infective larvae of *L. cincinnalis* are available (Junker, 1996; Riley & Huchzermeyer, 1996), we present only the main measurements of infective larvae examined in this study.

Primary larvae

The primary larvae (Figures 2C,D, 3D) have a distinct penetration apparatus located in front of the U-shaped mouth ring, in the anterior part of the body. It consisted of a lancet-shaped median stylet and 2 lateral stylets. The latter were split into a Y-shaped tip with 2 blades. Two pairs of stubby limbs were double-hooked and the tip of the tail carried 2 minute chitinous terminal thorns. Curled larvae measured 101 ± 7 μm (n = 11), but reached 122 ± 9 μm in length when the double-hooked tail was extended. The width of the primary larvae taken midway between the front and the hind pair of limbs averaged 60 ± 5 μm.

Eggs

The eggs of *L. cincinnalis* (Figure 2C,D) consisted of 2 membranes: a spherical outer shell, 233 ± 14 μm in diameter which surrounded a hyaline substance; and an ovoid inner membrane, 103 ± 13 μm long and 80 ± 7 μm wide, which enclosed the primary larva.

Of the eggs recovered from the posterior part of the uterus, 64% contained fully-developed primary larvae, of which 19% hatched when warmed to 30°C. When placed into a hypertonic sugar solution the eggs lost their spherical shape and shrivelled up. Depending on the time of exposure, eggs would swell up again when transferred back into regular tap-water.

Primary larvae hatched in 2 stages. Using its penetration apparatus and the claws, the primary larva started tugging at the inner membrane until it broke. Subsequently, the larva stretched to its full length, unfolding its ventrally curved tail, and started random movements which split the outer egg membrane lengthwise, setting the larva free.

Movements during the migration through host tissue were stereotyped, and fore and hind extremities were used alternately. While the anterior pair of limbs pulled towards the body, the posterior limbs moved away from the body in a downward motion. Subsequently, the hind limbs were brought back to the ventral side and the anterior limbs were spread widely. At the same time the tail alternately stretched and curled ventrally.

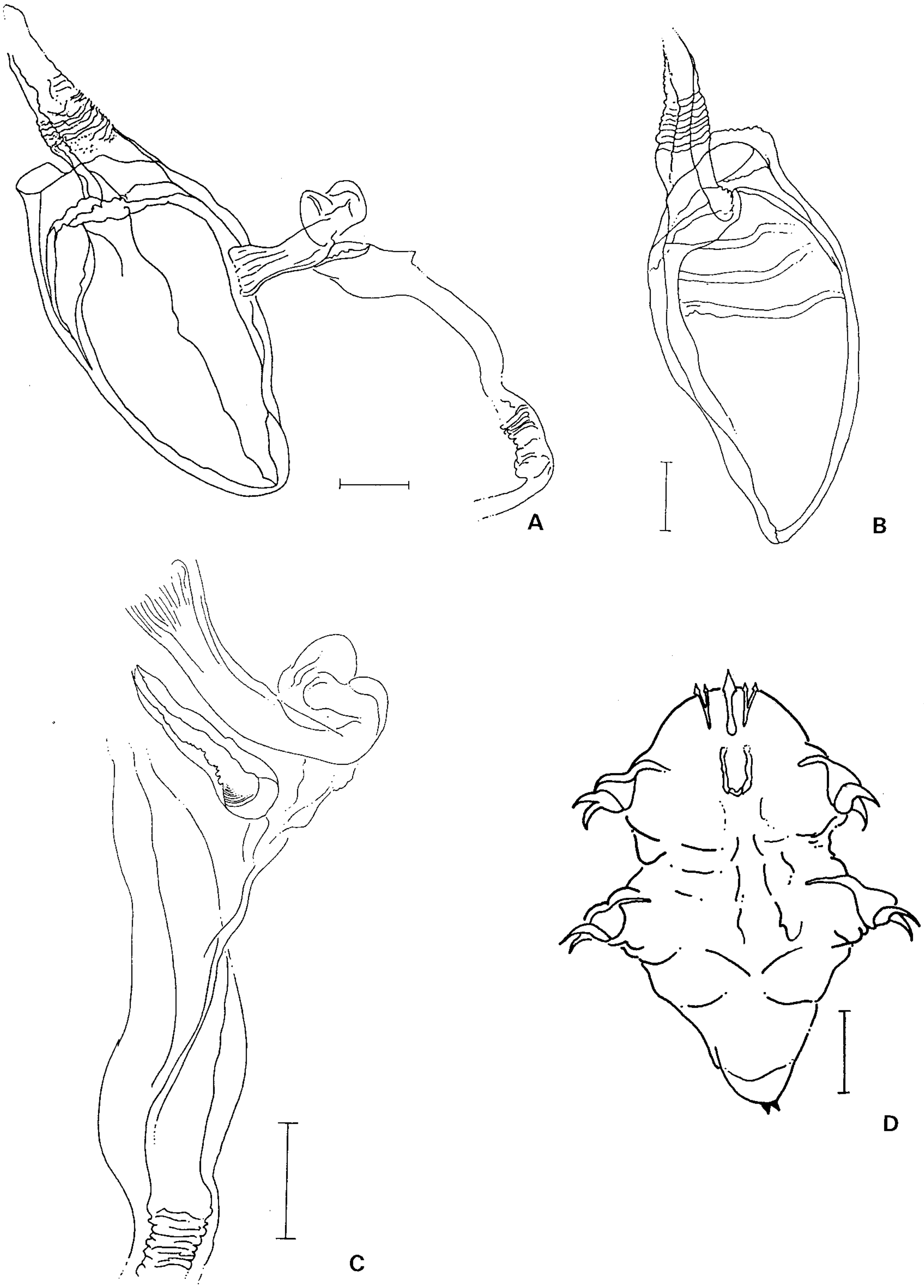

Figure 3. A. Right copulatory spicule and cirrus tip (No. 4.18/98). B. Left copulatory spicule (No. 2.3/98). C. Detail of cirrus tip (No. 4.27/98). D. Primary larva showing the penetration apparatus, the U-shaped oral cadre, the clawed limbs and the tail carrying two minute terminal thorns. *Scale-bars*: A-C, 100 μm; D, 25 μm.

Table 5. The main characteristics of the infective larvae of *Leiperia cincinnalis* recovered from Nile crocodiles from the Shimuwini Dam and from cichlids from the Phabeni Dam in the Kruger National Park in 1995 (LM19, LM20). For comparison additional data are included (Riley & Huchzermeyer, 1996; Junker, Boomker & Booyse, 1998a). All measurements are in micrometres unless otherwise indicated.

Source	Specimen number	Number of annuli	Body length (mm)	Mouth dimensions			Hook dimensions	
				Overall length	Cadre length	Width	Hook length	Fulcrum length
This paper	CW12.2	105	35	447	343	146	290	577
	CWA1	99	22	416	291	117	250	577
	CWA2	105	38	NM	NM	NM	299	563
	CWA3	104	31	424	333	130	262	622
	CWA4	98	23	421	296	125	256	517
	CWA5	105	25	471	341	140	287	587
	CWA9	104	30	437	322	153	278	609
	CWH4	106	28	437	333	138	265	561
	Average	103	29	436	323	136	273	577
	SD	3	6	19	21	13	18	32
Junker, Boomker & Booyse (1998a)	LM19	100	22	377	281	120	243	545
	LM20	NM	27	406	315	133	287	567
Riley & Huchzermeyer (1996)	F1832	106	21	400	285	113	270	620
	F1832	107	22	NM	NM	NM	280	650
	F1832	106	22	420	310	125	260	550

NM, not measured.

Discussion

Leiperia cincinnalis was the dominant pentastome species in the three crocodiles from the Silwervis Dam, but the intensity of infection was variable. Infective larvae and pre-adults recovered from the pulmonary artery accounted for most of these infections (Table 2).

The development of *L. cincinnalis* in its final hosts has been largely speculative. Rodhain & Vuylsteke (1932) described tufts of double- as well as single-hooked larvae attached to the aorta of a crocodile from the Congo. Their reference to the genital apparatus being more developed in the single-hooked specimens suggested the presence of males, but, unfortunately, these authors did not describe them. Rodhain & Vuylsteke (1932) discussed the possibility of an obligatory developmental phase in the circulatory system, but thought it exceptional rather than the rule. That it is indeed a specific pattern of development within the genus of *Leiperia* has since been confirmed in *L. australiensis* and by this study. We recovered infective larvae, as well as young females, from the lungs. Thus the lungs are a route of migration for the infective larvae on their way to the cardio-vascular system and for the adults on their way to their attachment sites in the trachea. Considering the high numbers of infective larvae and young adults often encountered in the pulmonary artery, the question arises why comparatively few adults are found in the trachea. This is especially true for the males, which occur in substantial numbers in the cardio-vascular system, but hardly ever in the trachea or lung. The relatively shorter life-span of male versus female pentastomes may partly explain this (Riley & Self, 1980; Riley, 1986; Junker et al., 1998b). Whether the majority of pre-adults get lost during migration, or whether an immune reaction from the host reduces their number, will remain speculative until more extensive studies can be undertaken.

A male and a female *L. cincinnalis*, recovered from one crocodile were attached next to each other in the trachea and probably had been *in copula* but were separated during recovery. We conclude that *L. cincinnalis* copulate in the trachea and not in the circulatory system; Riley & Huchzermeyer (1996) had already stated their doubts as to the likelihood of such a difficult procedure taking place in the narrow surroundings of the pulmonary artery.

We have found males with single hooks and completely developed copulatory spicules still encased in the cuticle of the infective larva in the pulmonary artery and this supports the speculation of Riley & Huchzermeyer (1996) that only one moult is necessary for the infective larva to develop into a fully adult male. However, another fully mature male surrounded by both the cuticula of the infective larva and the cuticula of a preceding single-hooked stage indicates that the males of *L. cincinnalis* undergo at least one additional moult after having reached sexual maturity. Unlike moulting in females, moulting in the males does not seem to be related to any further growth. Specimen No. 4.18/98, in addition to the male recovered from the trachea, was well within the range of the measurements of the other males (Table 4). Once again, these data emphasise the variability of structures encountered when dealing with pentastomes as already stated by Riley & Huchzermeyer (1995).

Riley & Huchzermeyer (1996) compared the hook morphology of females of *L. cincinnalis* from Uganda and the Congo. While both Ugandan specimens had flat-topped hooks, the hooks of the two Congo specimens, one of them described by Fain (1961), were characterised by a dorsal notch. Riley & Huchzermeyer (1996) speculated that the difference in hook morphology might indicate geographical variation, pointing out that the data set was too small to draw any final conclusions.

Our collection comprises male and female *Leiperia*, some of which carry flat-topped hooks and some of which possess hooks with a dorsal notch; sometimes both hook types occur in the same specimen. Visibility of the dorsal notch in the hooks can be influenced by the orientation of the hooks under cover-slip pressure and, especially in females, it becomes more prominent as specimens mature and grow. The dorsal notch is generally more distinct in the females than in the males. Measurements of the males and females were relatively uniform, especially the dimensions of the copulatory spicules, and gave no indication of the presence of two species. Our findings suggest that all the specimens belong to *L. cincinnalis*.

This, however, does not exclude the existence of a second *Leiperia* species in Africa, especially in view of the fact that the flat-topped hooks of the Ugandan specimens were considerably larger than the notched hooks of specimens collected from South Africa. The size of the hosts, as well as the intensity of infection, may influence the final size reached by the parasites, but our data do not support this speculation. Morphometric analysis of mature females taken from the heavily infected crocodile from the Shimuwini Dam, from the moderately infected Crocodile 4/98, and from the lightly infected Crocodile 2/98 did not differ substantially. Unfortunately, the oral cadres of the *Leiperia* from Uganda could not be measured and no male specimens were available for comparison.

In terms of gross morphology, the copulatory spicules of the *L. cincinnalis* males examined during this study and those of *L. australiensis* are very similar (Riley & Huchzermeyer, 1996). The cirrus tip in particular is very distinctive. The collar around the spatulate extension of the copulatory spicules of *L. cincinnalis* does not extend as far as the double collar found in *L. australiensis*. While the copulatory spicules of *L. cincinnalis* are larger than the ones of *L. australiensis*, the hook and mouth dimensions are quite similar.

Fish have long been known to be the intermediate hosts for *L. cincinnalis* (Fain, 1961) and field studies indicate that the infection with pentastomes has no adverse effect on the development of the intermediate host (Junker et al., 1998a). We believe that two factors are responsible for the high mortality of the experimentally infected *O. mossambicus*. These fish had a fungal infection that was aggravated by stress experienced during the experimental infection. Furthermore, we are convinced that the damage caused by the tissue migration of the hatched primary larvae contributed substantially to the subsequent death of the fish. This was especially true where 10 or more primary larvae were present.

It has been reported that porocephalid females shed a relatively high number of eggs per day, all of which contain fully-developed primary larvae (Riley, 1981, 1986). Junker et al. (1998b) recovered 3,400 eggs, 70% of which contained fully-developed, active primary larvae, from a single female *Sebekia wedli* Giglioli, 1922 that had been placed into phosphate buffered saline for one hour. While this figure is impressive, we are of the opinion that our experimental fish were exposed to a concentration of eggs that they would not normally encounter.

Once the eggs have been ingested by a suitable host, hatching of primary larvae seems to be a highly successful process, as most of the eggs recovered intact from fish did not contain fully-developed larvae.

The eggs of *L. cincinnalis* offer maximum protection for the primary larvae during the transition between the final and the intermediate host. Eggs are passed into the water via the faeces or sputum and depend entirely on chance ingestion by a bottom-feeding fish. The inner vitelline membrane is tough and it takes a considerable effort on the part of the primary larva to rupture it. Our findings suggest that the hyaline substance surrounding the inner shell protects the larva; however, the egg-shells are too thin to offer lasting protection from desiccation once removed from their natural aquatic environment.

Several authors have shown that pentastome eggs are in fact very resistant to environmental influences. Salazar (1965) found a high resistance towards acids and preservatives. Bosch (1987) reported that eggs maintained in physiological solution at 4–8°C remained infective for more than three months and assumed that high temperatures and dehydration were the main factors in killing larvae.

The eggs of *L. cincinnalis* began to hatch under cover-slip pressure when warmed to 30°C and needed no additional stimuli. Increase in temperature has the same effect in the pentastomid genera *Elenia* Heymons, 1932 (Porocephalida) and *Raillietiella* Sambon, 1910 (Cephalobaenida) (Bosch, 1987), but in *Reighardia sternae* (Diesing, 1864) Ward, 1899 (Cephalobaenida) hatching occurred only at 40°C (Banaja, James & Riley, 1975). These data reflect the physiology of their respective hosts. *R. sternae* has a direct life-cycle in homoiothermic seabirds (Banaja et al., 1975), which maintain a constant body-temperature of 37–41°C (Eckert, 1993), whereas the intermediate hosts of *Leiperia*, *Elenia* and *Raillietiella* are heterothermic.

The eggs of *L. cincinnalis*, as well as the hatching of the primary larva and subsequent movements during tissue migration, conform largely to those of *Porocephalus crotali* (Humboldt, 1808) Humboldt, 1811 of the Louisiana muskrat (Penn, 1942). It appears that the primary larvae of pentastomes are capable of generalised, very basic and stereotyped movements that are nevertheless sufficient for simple tissue migration from the alimentary tract into tissues.

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Description of *Pelonia africana* n. g., n. sp. (Pentastomida: Sebekidae) from the lungs of *Pelomedusa subrufa* and *Pelusios sinuatus* (Chelonia) in South Africa

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ABSTRACT

JUNKER, K. & BOOMKER, J. 2002. Description of *Pelonia africana* n. g., n. sp. (Pentastomida: Sebekidae) from the lungs of *Pelomedusa subrufa* and *Pelusios sinuatus* (Chelonia) in South Africa. *Onderstepoort Journal of Veterinary Research*, 69:53–59

The terrapins *Pelomedusa subrufa* and *Pelusios sinuatus* taken from a water reservoir in the Northern Province, South Africa, were examined for pentastome infections. Two immature specimens, a patent female and a mature male, were obtained from the lungs of four hosts, each of which harboured a single specimen. Based on the morphology of the specimens the new monospecific genus, *Pelonia africana* n. g., n. sp., is described. It is characterized by smooth, dorsally convex hooks with sharply bent blades. The oral cadre is more or less U-shaped. Delicate chitinous fibres, which can be difficult to see, connect the lateral prongs anteriorly. In this, as well as the morphology of the copulatory spicules, it is most like *Sebekia wedli*. The latter, however, possesses spinous hooks, which are absent in *P. africana.* The hooks are slightly and the copulatory spicules markedly larger in *P. africana* than in *S. wedli*. The lack of a double-hooked collar at the terminal end of the cowry-shell shaped base of each copulatory spicule and the absence of a peg-like extension of the oral cadre into the oesophagus, distinguishes *P. africana* from members of the genus *Alofia*.

The oral cadre of the South American species *Diesingia megastoma*, from aquatic chelonians, is more than twice the size than that of *Pelonia* and there is a distinct difference in shape. The hooks of the genus *Diesingia* are flat-topped, and both the anterior as well as the posterior fulcra carry cowl-like extensions. The number of annuli, 55–60 in *D. megastoma* and approximately 30 in *P. africana*, further separates the two genera. The most striking feature of *Diesingia* which sets it apart from *Pelonia* and the other genera of the family Sebekidae, is the configuration of its copulatory spicules.

Pelonia and *Diesingia* share morphological features with all the other sebekiids, but it is the unique combination of diagnostic characters that separates the two genera from those, as well as from each other.

Keywords: Chelonia, *Pelomedusa*, *Pelonia africana*, *Pelusios*, pentastomes, terrapins

INTRODUCTION

The majority of the six genera comprising the family Sebekidae Fain, 1961 occur exclusively in crocodilians. However, it has been speculated that a single species of the genus *Sebekia* Sambon, 1922 may also reach maturity in piscivorous turtles (Dukes, Shealy & Rogers 1971). Until now, only the South American genus *Diesingia* Sambon, 1922 has been known to be exclusive to a chelonian definitive host (Sambon 1922; Heymons 1941; Over-

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street, Self & Vliet 1985; Riley 1994) and, generally speaking, information on the pentastome fauna of tortoises, terrapins and turtles is scarce.

Fain (1961) refers to a nymphal pentastome found encysted in the liver of *Kachuga lineata*, a semi-aquatic oriental tortoise, which Hett (1924) assumed to be the infective larva of *Subtriquetra megacephala* (Baird, 1853) Sambon, 1922. The latter genus belongs to the family Subtriquetridae Fain, 1961, which is also believed to be exclusive to crocodilians (Riley 1986; Winch & Riley 1986; Junker, Boomker & Booyse 1998a). In addition, some five genera of terrapins from North America have been reported to harbour nymphs of *Sebekia mississippiensis* Overstreet, Self & Vliet, 1985, a crocodilian pentastome described from the American alligator, *Alligator mississippiensis* (Dukes *et al*. 1971; Boyce 1985; Overstreet *et al*. 1985). Significantly, all the literature cited above pertains to nymphal developmental stages of pentastomes.

It would appear that *Diesingia megastoma* (Diesing, 1836) (Sambon, 1922) is currently the only pentastome of which mature specimens have been recovered from the chelonian hosts, *Hydromedusa tectifera* and *Phrynops geoffroanus* (= *Hydraspis geoffroyana*) from Brazil (Diesing 1836; Heymons 1941; Self & Rego 1985; Da Fonseca & Ruiz 1956). The authors are not aware of any publications dealing with adult pentastomid parasites of chelonians from any other continent.

In this paper a pentastome from the lungs of two South African terrapins, *Pelomedusa subrufa* and *Pelusios sinuatus*, is described. *P*. *subrufa* occurs in pans, marshy areas and slow moving waters throughout southern Africa, and *P. sinuatus* inhabits large rivers and pans in the north-east of southern Africa. Both terrapins are omnivorous and fish form part of their diet (Patterson 1991).

Pelonia africana n. g, n. sp. shares morphological similarities with all the other genera of the family Sebekidae, but nevertheless possesses a unique combination of diagnostic criteria. Slide mounted specimens of *D. megastoma* were re-examined and found to be distinctly different from the pentastomes recovered from the South African terrapins. We thus consider it appropriate to erect a new genus to accommodate these specimens.

MATERIAL AND METHODS

In 2000 five *P. sinuatus* (host numbers Psin1–5) and a single *P. subrufa* (host number Psub1), with carapace lengths varying from 15–25 cm, were obtained from pans or marshy areas near the Arabie Dam, Northern Province. This dam is fed mainly by the Olifants River, but the Elands, Moses and Motsiphiri Rivers also feed into it (A. Hoffman, personal communication 2000).

Terrapins were either killed by intraperitoneal injection with sodium pentobarbitone (Eutha-naze™) or decapitated. The plastron and carapace were removed and the trachea, as well as the nasopharynx, were examined for pentastomes. The liver and heart were transferred into separate vials containing tap water, and the soft and delicate lungs were placed into a Petri dish, also containing tap water. Pentastomes were either dissected from the organs or collected from the tap water after they had migrated out of the organs. For morphological studies, pentastomes were fixed and preserved in 70 % ethanol and subsequently mounted in Hoyer's medium.

Three more pentastomid specimens, WIII/1, and Psub2/1 and Psub3/1 from the lungs of *P. sinuatus* and *P. subrufa* respectively, were collected during another unrelated study at the same locality and made available to us.

RESULTS

The nasopharynx and trachea of all hosts examined were free of pentastomes and hosts number Psin1, 3, 4 and 5 and Psub1 harboured no pentastomes at all. Single specimens of *P. africana* were recovered from the lungs of each of the remaining hosts. Premature females, without eggs in the uterus, were obtained from hosts WIII and Psin2. A gravid female collected from Psub2 contained eggs with fully developed primary larvae. A mature male was present in the lungs of Psub3.

Description of *Pelonia africana* n. g., n. sp. (Table 1)

TYPE HOSTS AND LOCALITY

Pelusios sinuatus and *Pelomedusa subrufa* from the Arabie Dam (24°53'S, 29°22'E), Northern Province, South Africa.

TYPE MATERIAL

Holotype male, no. T 2186 from *Pelomedusa subrufa*, allotype female, no. T 2187 from *Pelomedusa subrufa* and paratypes (immature) from *Pelomedusa subrufa* and *Pelusios sinuatus*, no. T 2188. All spec-

TABLE 1 Comparative measurements of *Pelonia africana* n. g., n. sp., *Diesingia megastoma* and *Sebekia wedli*. All measurements are given in micrometres unless otherwise stated

Specimen number	Body length (mm)	Number of annuli	Mouth dimensions			Hook dimensions		Copulatory spicules		
			Overall length	Cadre length	Width	Hook length	Fulcrum length	Total length	Cowry shell length	Width
WIII/1 (Paratype F, T 2188)	15	28	322	248	127	NM	NM	NA	NA	NA
Psin2/1 (Paratype F, T 2188)	13	27	313	216	133	115	239	NA	NA	NA
Psub2/1 (Allotype F, T 2187)	27	30a	380	301	182	NM	NM	NA	NA	NA
Psub3/1 (Holotype M, T 2186)	9	27	265	207	150	NM	NM	515	324	214
Diesingia megastoma M (After Heymons 1941)	7	70	NM	524	205	NM	NM	NM	NM	NM
Diesingia megastoma M (After Heymons 1941)	6	70	NM	496	180	140	NM	NM	NM	NM
Diesingia megastoma F (After Self & Rego 1985)	10	65	NM	670	380	140*	520	NA	NA	NA
Sebekia wedli F (After Riley & Huchzermeyer 1995a)	15–19	NC	355	229	121	80	176	NA	NA	NA
Sebekia wedli M (After Riley & Huchzermeyer 1995a)	8	NC	212	136	76	59	134	310	213	115

F	Female
M	Male
NA	Not applicable
NC	Not counted
NM	Not measured
*	Only the length of the blade was measured

imens are mounted in Hoyer's medium and deposited in the National Animal Helminth Collection, ARC-OVI, Onderstepoort, South Africa.

Etymology

Pelonia has been named after its two host species that belong to the family Pelomedusidae which comprises freshwater chelonians from Africa, Madagascar and southern Australia.

Description

The body is claviform, the abdomen being widest in the anterior third and tapering to a bluntly rounded caudal tip. Ventrally the small trapezoid cephalothorax is continuous with the ventrally flattened abdomen but dorsally demarcated from the remainder of the body. A small number of wide annuli are present.

Female

The strongly chitinised oral cadre is more or less U-shaped, the gap between the lateral prongs only slightly narrowing anteriorly. Muscle contraction or the amount of pressure applied when mounting, can result in a more ovoid profile. The oral cadre appeared to be open anteriorly as the delicate chitinous fibres connecting the two sides were difficult to see. A heavily chitinised, bowl-shaped base unites the two lateral prongs posteriorly (Fig. 1B, C). The oral cadre of the allotype female was slightly larger than that of the two immature specimens, WIII/1 and Psin2/1.

The smooth hooks are dorsally convex with a slight dorsal notch where the strongly curved blade emerges from the base (Fig. 1F). The configurations of the posterior and anterior hooks appear to be identical and are supported by strong fulcra. Unfortunately, measurements could only be made from a single hook from an immature female.

It was not possible to decide whether the females were heterogynous, with the utero-vaginal pore being situated one or two annuli anteriorly from the anus, or ophistogynous. The eggs of *P. africana* consist of a spherical outer membrane, 183 ± 8 mm in diameter that surrounds a hyaline substance and an ovoid inner eggshell, 96 ± 7 µm long and 70 ± 4 µm wide (Fig. 1G), that encloses the primary larva.

Male

Although the oral cadre of the male is slightly smaller than those of the two immature females (Fig. 1A), its general morphology, as well as that of the hooks and the fulcra, is similar to that of the females. The paired copulatory spicules are heavily sclerotised and cowry-shell shaped (Fig. 1D). The anterior spatulate extension carries rows of rounded, chitinous teeth, which become progressively indistinct towards the tip (Fig. 1E).

DISCUSSION

The body-shape of *P. africana* corresponds closely to the illustration of a mature female of *D. megastoma* from *H. tectifera* (Self & Rego 1985). One of the main differences between *P. africana* and *D. megastoma* lies in the oral cadre. That of *D. megastoma* is more than twice the length and width than that of the African species. Own observations show the oral cadre of *Diesingia* to carry a small peg-like extension into the oesophagus, not unlike that of the genus *Alofia* Giglioli, 1922, which is absent in specimens of *Pelonia*. Furthermore, the prominent bowl-shaped chitinous structure at the base of the oral cadre of the latter genus is absent in *Diesingia*.

Both genera of chelonian pentastomes possess smooth hooks. However, the fulcra of *Pelonia* are devoid of any extensions, while the fulcra of *Diesingia* are furnished with cowl-like extensions, similar to those seen in the genus *Selfia* (Riley 1994). The hooks of *D. megastoma* appear to be flat-topped with a sharply curved blade, demarcated from the shank by a single notch (Self & Rego 1985), while those of *P. africana* are dorsally convex and marked by a slight dorsal notch.

So far, no conclusive description of the copulatory spicules of *Diesingia* has been given, and the two male specimens we examined, possess copulatory spicules that are unique among the members of the family Sebekidae. The cowry-shell shaped base and the long spatulate extension of the open side are reminiscent of other sebekiid genera (Riley, Spratt & Winch 1990), but the shorter of the two anterior extensions has been transformed into a tiller-like, chitinous spike.

The genus *Pelonia* is distinct from the genus *Diesingia*, and represents the first record of a new genus of pentastomes exclusive to chelonian final hosts from the African continent.

Pelonia africana is similar to the African crocodilian pentastome *Sebekia wedli* Giglioli, 1922 in Sambon, 1922. This is especially true for the oral cadre, which in the latter species is also approximately U-

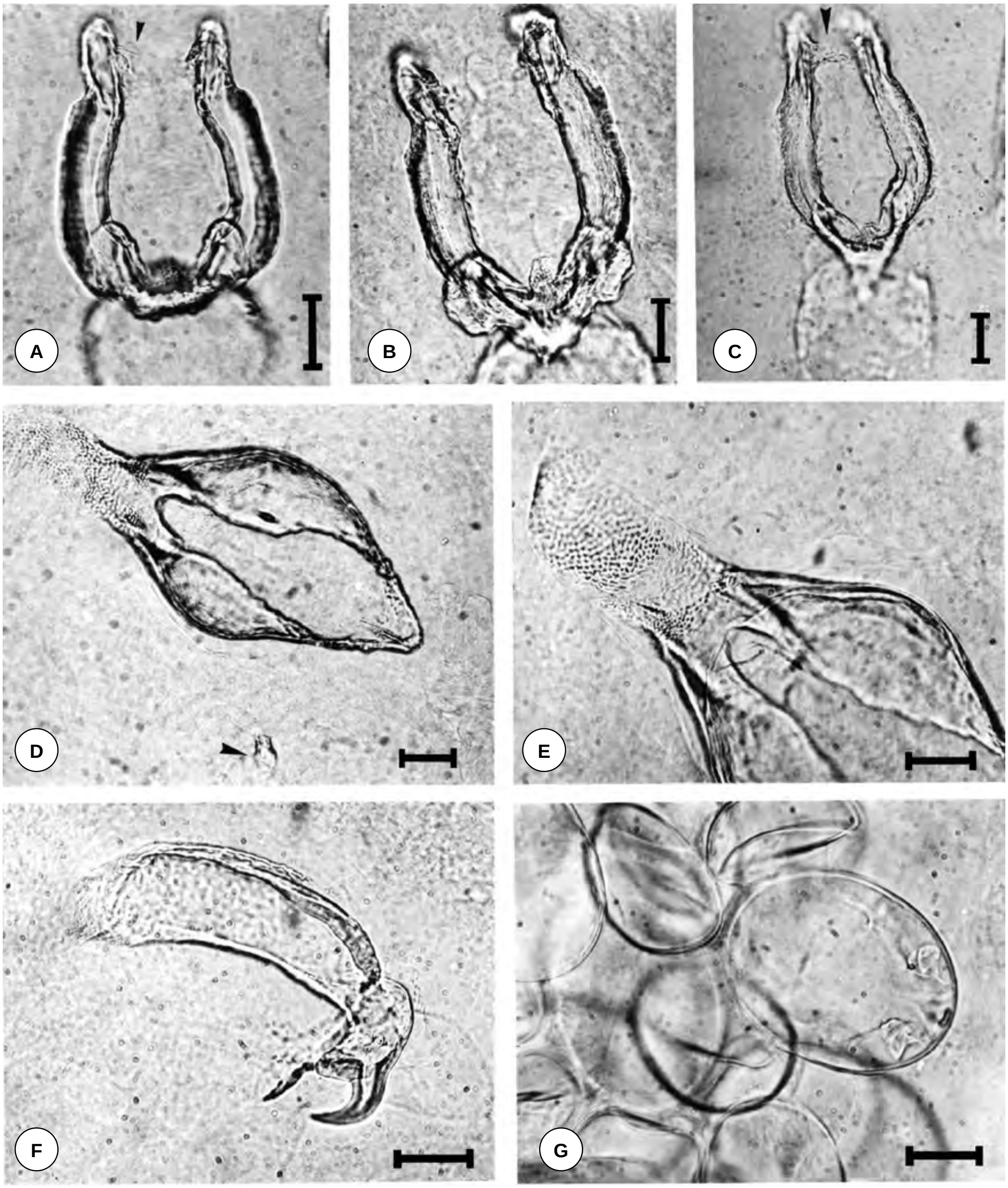

FIG. 1 *Pelonia africana* n. g., n. sp.

A Oral cadre of holotype male. The delicate chitinous fibres connecting the lateral prongs of the oral cadre anteriorly are partly visible (arrow). Scale bar: 50 mm

B Oral cadre of the allotype female. The anterior chitinous bridge is not visible in this photograph. Scale bar: 50 mm

C Oral cadre of an immature female. The chitinous fibres connecting the lateral prongs are clearly visible (arrow). Scale bar: 25 mm

D Ventral view of the right copulatory spicule of the holotype male. It is obpyriform and the spatulate extension carries small chitinous teeth. The arrow marks a chitinous part of the cirrus. Scale bar: 50 mm

E Detail of the left copulatory spicule

F Right posterior hook of an immature female. Scale bar: 50 mm

G Egg with fully developed primary larva. Scale bar: 50 mm shaped, and because of an almost invisible, very delicate anterior bridge of chitin, it seems to be open anteriorly (Riley & Huchzermeyer 1995a). A comparison of measurements, however, shows the buccal complex of *S. wedli* to be slightly smaller than that of *P. africana* (Riley & Huchzermeyer 1995a, Junker, Boomker & Booyse 1998b). The copulatory spicules of male *P. africana* are strongly reminiscent of *S. wedli*, and they could easily be confused, in that both are obpyriform and carry chitinous teeth on the spatulate extensions. Nevertheless, the spicules of *P. africana* are markedly larger than those of *S. wedli* (Riley & Huchzermeyer 1995a).

The main distinguishing character between *P. africana* and *S. wedli* is the absence of the prominent spines on the dorsal hook surface. The lack of anterior extensions to the fulcra further serves to separate *Pelonia* from the other species of the genus *Sebekia* as defined by Riley *et al*. (1990).

Superficially, the aspinose hooks, the curve of the blade and the shape of the oral cadre might lead to confusion of *P. africana* with the *Alofia* spp. The copulatory spicules of *P. africana*, however, lack the double-hooked collar diagnostic for *Alofia* and the genus *Selfia* Riley, 1994 (Riley 1994). Moreover, the oral cadre neither possesses the distinct, open *Alofian* U-shape nor the peg-like extension into the oesophagus (Riley & Huchzermeyer 1995a, b; Junker, Boomker & Bolton 1999).

Recently *Agema* Riley, Hill & Huchzermeyer, 1997, a new pentastomid genus, has been described from African dwarf crocodiles, *Osteolaemus tetraspis osborni*, and slender-snouted crocodiles, *Crocodylus cataphractus* (Riley, Hill & Huchzermeyer 1997). While the hooks of *P. africana* exhibit the already mentioned abrupt right-angle bend near the base, those of *Agema* are very smoothly curved and the ovoid oral cadre of the latter genus is closed anteriorly by prominent chitinous crescents (Riley *et al*.1997).

Pelonia africana morphologically resembles especially the genus *Sebekia* and to a lesser extent the genus *Alofia*. Heymons (1941) pointed out the similarity between *D. megastoma* and its South American sebekian and alofian counterparts. Therefore there is a strong case for the inclusion of the genera *Pelonia* and *Diesingia* into the family Sebekidae, as was suggested for the latter genus by Riley (1993). The fact that all sebekiid genera have a similar life-cycle using fish as intermediate hosts and semi-aquatic definitive hosts (Fain 1961; Riley 1986, 1994; Riley *et al*. 1997) indicates a close relationship between the two genera parasitising chelonians and those of crocodilians.

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Redescription of *Diesingia megastoma* (Diesing, 1836) Sambon, 1922, a pentastomid parasite from the South American terrapin *Hydromedusa tectifera* Cope

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Abstract

Slide-mounted material of the pentastomid parasite *Diesingia megastoma* (Diesing, 1836) Sambon, 1922 from the South American chelonian *Hydromedusa tectifera* Cope is reviewed and the perfunctory, often omissive, description of the species is amended. The strong morphological similarities between *D. megastoma* and the crocodilian and chelonian pentastome genera of the family Sebekiidae Sambon, 1922, *Alofia* Giglioli, 1922, *Selfia* Riley, 1994, *Sebekia* Sambon, 1922, *Agema* Riley, Hill & Huchzermeyer, 1997, *Leiperia* Sambon, 1922 and *Pelonia* Junker & Boomker, 2002, clearly place *Diesingia* Sambon, 1922 within the same family. However, the unique combination of its main diagnostic criteria makes *Diesingia* a distinct genus. The absence of an elaborate, flared cirrus-tip in *D. megastoma* distinguishes it from *Leiperia*, while emphasizing its similarity to the remaining genera mentioned above. *D. megastoma* resembles *Alofia* in that it possesses smooth, flat-topped hooks and an anteriorly open oral cadre with an oesophageal peg. The copulatory spicules of *Diesingia*, however, lack the double-hooked collar, typical for *Alofia* and *Selfia*. Unlike the peg-like extension of the fulcra of the hooks of *Sebekia*, that of *D. megastoma* is cowl-like and carries spines only on the anterior fulcra. Moreover, the hooks of *Sebekia* are usually convex and spinose and the ovoid oral cadre is closed anteriorly. *Diesingia* differs from *Pelonia* through the latter's smooth but dorsally convex and extension-free hooks. The copulatory spicules of *Pelonia* and *Agema* are reminiscent of the basic build found in *Sebekia*, whereas in *D. megastoma* the short, ventral extension of the cowry shell-shaped base of the copulatory spicules has been transformed into a structure resembling the collembolan fulcrum. The latter is connected to the base via a joint, a configuration which is unique in the Sebekiidae.

Introduction

Despite their discovery more than one-and-a-half centuries ago, the present knowledge on pentastomes parasitising chelonian final hosts is scant. A single species, *Diesingia megastoma* (Diesing, 1836) Sambon, 1922, from South American terrapins was recognised. It was first described from two adult males recovered from the lungs of a Geoffrey's side-necked turtle *Phrynops geoffroyanus* (Schweigger) (syn. *Hydraspis geoffroana*) in Brazil by Diesing as *Pentastoma megastomum* Diesing, 1836 (Diesing, 1836; Sambon, 1922; Fain, 1961). Since then, it has caused much confusion. The two original specimens, kept at the Museum of Natural History at Vienna, have been renamed and re-examined by several authors. Leuckart (1860), referring to Diesing's (1836) description only, changed the name to *Pentastomum megastomum*, while Shipley (1898) ex-

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amined the Vienna specimens himself. Without adding much detail to the initial, very superficial description, Shipley (1898) redescribed them as *Porocephalus megastomus*, a name previously given to them by Stiles (1893, in Sambon 1922) in accordance with the then common trend to include the majority of the exotic pentastomes in *Porocephalus* Humboldt, 1811 (Heymons, 1941).

When Sambon (1922) reviewed the known pentastomid genera, Diesing's type-specimens no longer fitted the diagnostic criteria of the genus *Porocephalus* and he suggested the inclusion of *P. megastomum* in the new genus *Diesingia* Sambon, 1922. This genus had been created to accommodate *D. kachugensis* Sambon, 1922 from the liver of *Kachuga kachuga* (Gray) (syn. *K. lineata*), a semi-aquatic oriental tortoise. Riley (1986) pointed out that Hett (1924, in Fain, 1961) considered *D. kachugensis* to be the larval stage of *Subtriquetra megacephala* (Baird, 1835) Sambon, 1922, a crocodilian pentastome. Heymons (1941) was the first author to provide a more detailed description of the type-specimens for which the name *D. megastoma* had become accepted, and included measurements and drawings of the hooks and the oral cadre. Da Fonseca & Ruiz (1956) created *Butantanella* Da Fonseca & Ruiz, 1956 to accommodate *D. megastoma* and the specimens of a collection of pentastomes recovered from the lungs of 15 *Hydromedusa tectifera* Cope from Brazil.

Self & Rego (1985) examined pentastome specimens from collections from the Instituto Oswaldo Cruz and from the British Museum (Natural History) Collection. These included fully mature males and females from the lungs of the Brazilian terrapins, *H. tectifera* and *P. geoffroanus*, and Self & Rego (1985) concluded that these were identical with Diesing's specimens. On morphological grounds, Self & Rego (1985) reclassified *D. megastoma* as *Sebekia megastoma*, dismissing Da Fonseca & Ruiz's (1956) previous classification.

The uncertainty surrounding its type-species led to considerable confusion as regards the systematic status of the genus *Diesingia*. Fain (1961) included it in the family Sebekiidae Sambon, 1922, whereas Riley (1983), in an outline classification of the pentastomes, placed the genus separately, directly following the genera of the family Sambonidae Fain, 1961, substituting the family name by a question mark. Subsequently, Self & Rego (1985) abandoned *Diesingia* in favour of *Sebekia* Sambon, 1922, a view that was not adopted by Riley (1986), who created the monogeneric family Diesingiidae Riley, 1986. In a later publication, Riley (1994) placed *Diesingia* back in the family Sebekiidae.

In this paper slide-mounted specimens of *D. megastoma*, collected from *H. tectifera* from Brazil, are described. Based on our findings, we support the validity of the genus *Diesingia* as well as its inclusion in the family Sebekiidae.

Materials and methods

All specimens described here were originally recovered from *H. tectifera* from Brazil by an unknown collector. The collection comprises slide-mounted specimens as well as specimens that had previously been fixed in formalin (Da Fonseca & Ruiz, 1956), but are now preserved in alcohol. These are, however, in an extremely poor condition and very brittle. The anterior and posterior hooks had been removed and mounted in Hoyer's medium several years ago and the bottle with alcohol specimens now contains only the abdomens of the specimens F2463-5, F2463-6 and KI-3. These are mature females, as evidenced by hook measurements and the egg-filled uteri of two specimens. The *D. megastoma* material studied comprises the following:

F2463-2. A male specimen, mounted whole and stained with a chromatin stain. The slide was originally labelled '*Butantanella megastoma*, from the Instituto do Butantan ex *Hydromedusa tectifera*' (see below).

F2463-3. A young female, mounted whole and originally identified as 'Butantan F 5960, *Butantanella megastoma* of the lung of *H. tectifera*, from the Paraná State, Brazil'. The slide is dated 7 December, 1951 and carries the names Da Fonseca & Ruiz.

We conclude that F2463-2 and F2463-3 are two of the specimens on which Da Fonseca & Ruiz (1956) based their description of *B. megastoma*. In fact, Da Fonseca & Ruiz (1956) stated that specimen 5960 forms part of a collection of male and female pentastomes taken from the lungs of 15 *H. tectifera* in August, 1951 at Tranqueira, Paraná State.

F2463-4. A male specimen. The abdomen, including the copulatory spicules, is mounted on one slide and a second slide contains the posterior and anterior hooks, as well as the oral cadre. The latter, however, is severely damaged.

F2463-5 and F2463-6. The hooks of two females were dissected out and the posterior and anterior hooks are mounted under separate cover-slips on the same slide. The oral cadres of both specimens have apparently been lost.

KI-3. The whole slide-mounted cephalothorax of a mature female.

All measurements were made according to the procedures described by Fain (1961), Riley, Spratt & Winch (1990) and Riley (1994).

Diesingia megastoma **(Diesing, 1836) Sambon, 1922**

Description (Figures 1,2)

The abdomens of 2 alcohol-preserved females are slender and elongate, with pointed caudal tips that appear slightly curled ventrally. Since the only intact specimens are slide-mounted, little else can be said about the body-shape. In the male specimens F2463-4 and F2463-2, as well as in the female F2463-3, a single row of chloride cells with prominent pore caps is present on the anterior border of each annulus.

Females (Table 1) According to its slide label, specimen F2463-6 was 1.5 cm in length prior to the dissection of hooks from its cephalothorax. The single prepatent female, F2463-3, has 55-60 annuli, but, since the caudal tip is slightly damaged accurate counting is difficult. The same specimen possesses smooth hooks with long, slender, canaliculate blades that are sharply curved. A slight, but distinct, notch demarcates the blade from the flat dorsal hook surface. While the anterior and posterior hooks are equal in size, the morphology of their fulcra differs in that all possess a cowl-like anterior extension, but that the cowl of the anterior fulcra is spinose, while those of the posterior ones are smooth (Figures 1E,F, 2C,D). The hooks of 3 mature females are distinctly larger but otherwise similar to those described above. The cowl of the fulcrum is not always readily visible. The posterior hooks of specimen F2463-6 display the cowl clearly (Figure 2D) and a structure next to one of the anterior hooks is assumed to be the broken-off spinose extension of the fulcrum. The second anterior hook of specimen F2463-6 and the hooks of specimens F2463-5 and KI-3 are in too poor a condition to observe any extensions to the fulcra.

The oral cadre of the prepatent female is about half the size of that of KI-3, but otherwise similar in shape. Seen from a slightly lateral view, the overall profile is ovoid and the oral cadre is open anteriorly. A small peg-like extension into the oesophagus measures 23 μm in the young female (F2463-3) and 92 μm in specimen KI-3. The lateral prongs widen into chitinous lobes anteriorly (Figures 1B, 2A).

Males (Table 1) Specimen F2463-2 is 1.1 cm long and 58 annuli are present. The hooks of both males are more or less the same size as those of the young female and are morphologically similar. One of the anterior hooks of specimen F2463-4 has a spinose cowl of the fulcrum but no extensions could be seen in the remaining hooks. The hooks of specimen F2463-2 were too obscured by the dark stain to observe much detail.

The oral cadre of the male F2463-2 is slightly larger than that of the young female, F2463-3 and the peg-like extension into the oesophagus measures 60 μm (Figures 1A, 2B). Although seen ventrally, the shape of the oral cadre corresponds well with that of the female. Starting with a narrow base, the middle section of the oral cadre is slightly expanded, and narrows again towards the anterior end.

The copulatory spicules of the males consist of a cowry shell-shaped base from which 2 extensions protrude anteriorly (Figures 1C, 2F). The longer of the 2 extensions emerges ventrally, i.e. from the open side of the base. It consists of 2 lateral prongs that unite in the anterior half of the extension, to form a spatula. The distal half is reinforced by transverse cuticular ridges. The short extension emerges from an articulated joint at the closed dorsal side of the base. It is strongly reminiscent of the fulcrum found in collembolans and runs through the gap formed by the lateral prongs of the ventral extension (Figures 1D, 2E).

Discussion

Comparative measurements of *Diesingia megastoma* from the literature are presented in Table 2. The number of annuli counted by Heymons (1941) and Da Fonseca & Ruiz (1956) are slightly higher than those of Self & Rego (1985) and the present authors. We assume this variation to be a result of counting techniques as well as differences in the quality of the material. Heymons (1941) indicated, that the chloride cell pores of Diesing's two original specimens had become difficult to discern. Our counts exclude the tip of the tail, as well as the annuli on the cephalothorax that have incomplete rows of chloride cells.

Table 1. The main diagnostic characteristics of *Diesingia megastoma* (Diesing, 1836) from *Hydromedusa tectifera* Cope (Chelonia) from Brazil. In the case of the hooks and copulatory spicules, the figures on the left refer to the structures on the left and the figures on the right to the corresponding feature on the right side. All measurements are in micrometres.

Specimen no.	Sex	Oral cadre			Anterior hooks					Posterior hooks					Copulatory spicules		
		Overall length	Cadre length	Width	Hook length	Blade length	Base length	Plateau length	Fulcrum length	Hook length	Blade length	Base length	Plateau length	Fulcrum length	Cowry-shell length	Total length	Spike length
F2463-2	M	653	488	239	NM	NM	NM	NM	NM	166 NM	94 NM	60 NM	83 NM	281 NM	345 345	773 750	248 258
F2463-4	M	NM	NM	NM	184 NM	113 NM	58 NM	83 NM	373 NM	202 207	108 108	67 67	106 106	329 NM	303 363	754 741	184 235
F2463-3	F	570	446	207	163 NM	106 NM	62 NM	92 NM	334 NM	177 NM	99 NM	67 NM	104 NM	NM NM	NA	NA	NA
F2463-5	F	NM	NM	NM	260 258	143 136	108 97	145 154	442 451	244 246	147 140	99 94	133 147	NM NM	NA	NA	NA
F2463-6	F	NM	NM	NM	246 NM	136 NM	97 NM	133 NM	NM 506	255 253	124 131	87 101	147 145	NM NM	NA	NA	NA
KI-3	F	1081	814	NM	251 248	147 147	99 87	126 127	483 511	258 NM	138 NM	97 NM	145 NM	398 NM	NA	NA	NA

F, Female; M, Male; NA, Not applicable; NM, Not measured.

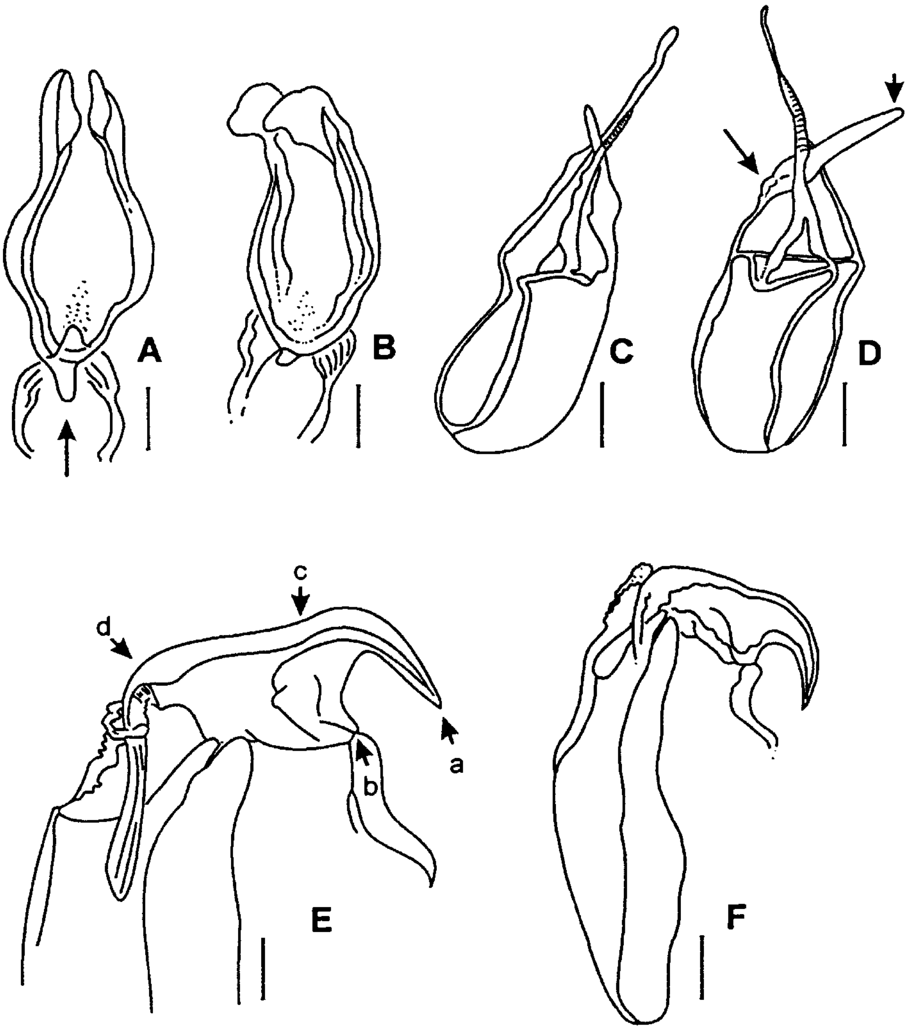

Figure 1. Diesingia megastoma. A. Ventral view of the oral cadre of male F2463-2 depicting the oesophageal peg (arrow). B. The oral cadre of female F2463-3 in ventrolateral view. The anterior chitinous lobes are prominent. C. Left copulatory spicule of F2463-4 seen ventrolaterally. D. Lateral view of the right copulatory spicule of the same male as in C. Note the cuticular ridges on the long spatulate extension. The shorter, fulcrum-like extension is jointed (large arrow); its length is the distance between the large and the small arrow. E. Posterior hook of female F2463-6 depicting the aspinose cowl-like extension of the posterior fulcrum. Points d and b are the points of insertion of the extensory and flexory musculature, respectively; Point c demarcates the notch in the dorsal hook surface. F. Anterior hook of female F2463-3. Note the spines on the cowl of the anterior fulcrum. *Abbreviations*: ac, blade length; ad, hook length; bc, base length; cd, plateau length. *Scale-bars*: A,B,C,D, 100 μm; E,F 50 μm.

According to Self & Rego (1985), the oral cadre of *D. megastoma* is closed anteriorly by fibres to form a ring. The same authors describe sharp anterior and posterior spurs that extend inwardly from the lateral prongs. Such structures were absent in the *Diesingia* material in the present study. Heymons (1941) described the oral cadre of *D. megastoma* as being U-shaped and open anteriorly, which is more in accordance with our findings. We believe the difference in shape of the oral cadre in Self & Rego's (1985) specimens to be due to a distortion caused by pressure while mounting the specimens. None of the previous descriptions (Heymons, 1941; Da Fonseca & Ruiz, 1956; Self & Rego, 1985) have mentioned the peg-like extension of the oral cadre into the oesophagus despite its being quite an obvious feature.

There is relatively little discrepancy in the description of the hooks of *D. megastoma* by earlier authors, all of which describe them as smooth, single and equal (Heymons, 1941; Da Fonseca & Ruiz, 1956; Self &

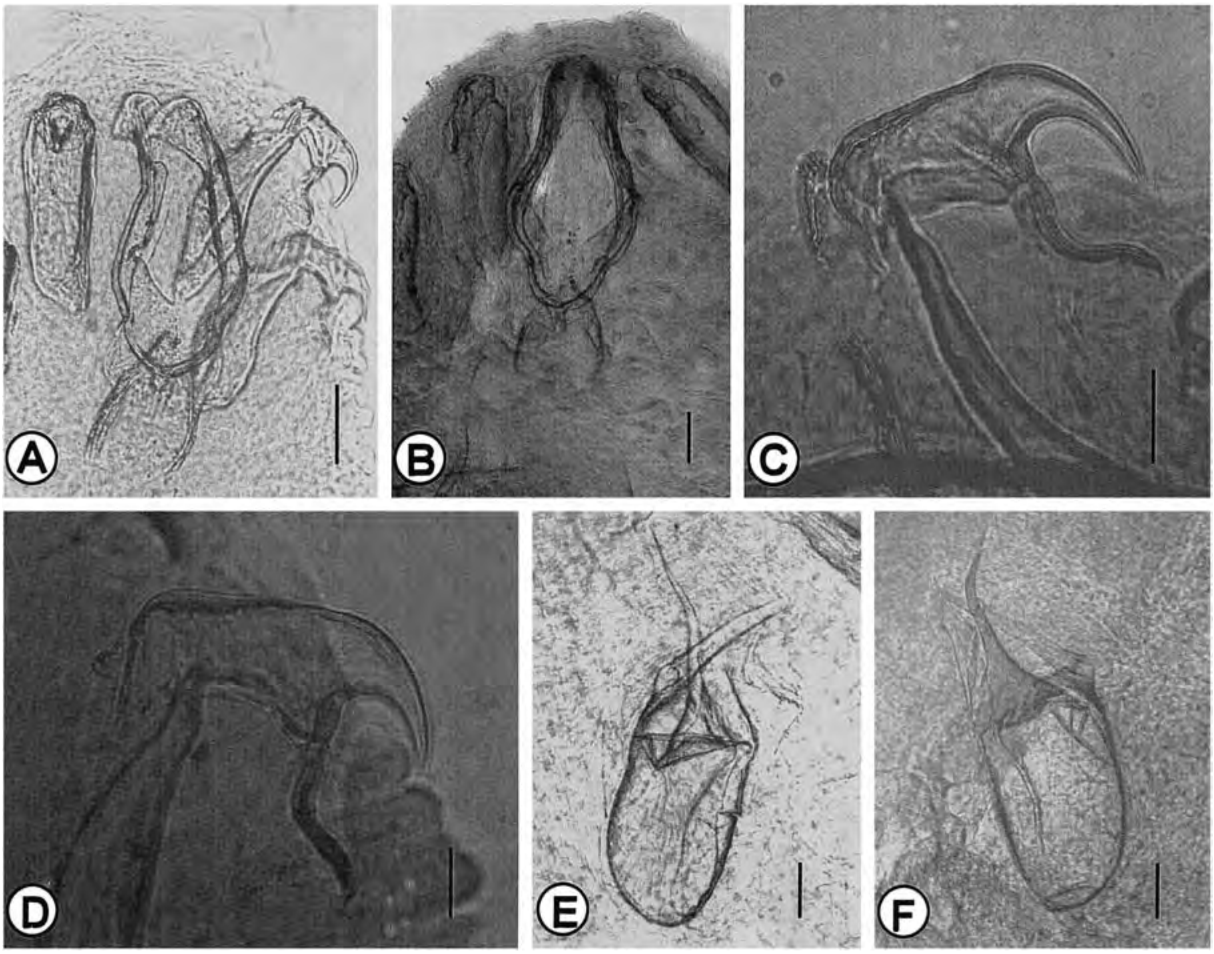

Figure 2. Diesingia megastoma. A. The oral cadre of female F2463-3. B. The oral cadre of male F2463-2. C. Close up of the left anterior hook of female F2463-3. D. Detail of the posterior hook of female F2463-6. E. Lateral view of the right copulatory spicule of male F2463-4. F. The left copulatory spicule of male F2463-4. S*cale-bars*: A, 120 μm; B,E,F, 100 μm; C,D, 50 μm.

Table 2. Comparative measurements of *Diesingia megastoma* (Diesing, 1836) found in the literature. All measurements are given in micrometres unless otherwise indicated.

Sex	Body length (mm)	Number of annuli	Oral cadre		Hooks				Source
			Cadre length	Width	Hook length (AD)	Blade length	Base length	Fulcrum length	
M	7	70	524	205	NM	NM	NM	NM	Heymons (1941)
M	6	70	496	180	140	NM	NM	NM	Heymons (1941)
F*	11 - 20	ca. 70	770	440	140?	140?	NM	550	Da Fonseca & Ruiz (1956)
F*	10	65	670	380	NM	140	110	520	Self & Rego (1985)

F, Female; M, Male; NM, Not measured.
*Combined data of several females; ?, It is not clear which of the two measurements the authors refer to.

Rego, 1985). Two shallow dorsal notches are visible in Heymon's (1941) drawing of a hook and, otherwise, it conforms well with that of Rego & Self (1985). In our experience, slight differences in the orientation of specimens on the slide on which they are mounted can interfere with the visibility of certain structural characteristics, and we attribute the fact that none of the above authors described the cowl-like anterior extensions of the fulcra to this.

Heymons (1941), as well as Self & Rego (1985), omitted the description of the copulatory spicules of the males, despite considering them fully mature specimens. This might be explained insofar as the true taxonomic value of these structures was only subsequently recognised (Riley, 1986). Unfortunately, Da Fonseca & Ruiz (1956) referred only briefly to the copulatory spicules of the males. However, their illustration of a slide mounted and stained male specimen depicts the characteristic outline of the copulatory spicules well. The latter authors provided a detailed description of the female reproductive organs and stated that the vulva is situated on a mammilliform protuberance on the 15th caudal annulus. Similarly, Self & Rego (1985) described the utero-vaginal pore as subterminal on a prominent papilla. These structures were not visible in neither the slide-mounted material or the alcohol-fixed remains of the female specimens.

The measurements of the oral cadre of one of the males in the present study and those of the two males examined by Heymons (1941) correspond well. The hooks of both males examined by us, however, are larger than the single measurement of Heymons (1941), although the author specifies that the hook length was measured from the tip of the blade to the insertion of the *musculus extensor unci*. There is a good correlation between the length of the blade and the length of the base in the hooks of mature females as determined by Self & Rego (1985) and our own data. Despite slight deviations, the measurements taken of the fulcra also appear uniform. The oral cadre of the single female measured in this study appears considerably larger than recorded by Self & Rego (1985) and Da Fonseca & Ruiz (1956). It is difficult to interpret the hook dimensions provided by the latter authors, as their terminology is not in accordance with that later defined by Fain (1961) and there are no explanatory illustrations. We do, however, believe that the length of the anterior and posterior hook refers to measurements of the blade only and we deduce that the term '*Bügel*' actually refers to the term fulcrum as it is used nowadays. We are in doubt as to the meaning of the term '*fulcrum*' as used by Da Fonseca & Ruiz (1956).

In addition to *Diesingia*, the crocodilian pentastome genera *Alofia* Giglioli, 1922 and *Sebekia*, represented by *A. platycephala* (Lohrmann, 1889) Giglioli, 1922 and *S. microhamus* Self & Rego, 1985, are also present in Brazil (Heymons, 1941; Self & Rego, 1985). The anteriorly open oral cadre of *D. megastoma*, and especially its oesophageal peg, is reminiscent of that of *Alofia*, but it is too oval in profile (Riley & Huchzermeyer, 1995a). The flat-topped, smooth, fang-like hooks are similar to alofian hooks, and it is mainly the presence of the anterior extensions of the fulcra which sets *Diesingia*'s hooks apart from the generic characteristics of *Alofia* (see Fain, 1961; Riley, 1994), although *A. parva* Riley & Huchzermeyer, 1995 has been described as possessing a spinose cowl-like extension to the anterior fulcrum (Riley & Huchzermeyer, 1995b). *S. microhamus* is atypical for the genus since it possesses aspinose hooks that are too small to be confused with those of *D. megastoma* (Self & Rego, 1985). The dorsally convex hooks of *Pelonia africana* Junker & Boomker, 2002 are smooth and the fulcra are without anterior extensions. Also, its oral cadre lacks the oesophageal peg (Junker & Boomker, 2002). However, the single most distinguishing characteristic of *Diesingia* from other sebekiid genera is the unique configuration of its copulatory spicules. The copulatory spicules of *Alofia* and *Selfia* Riley, 1994 are marked by the double-hooked collar terminating the shorter of the two anterior extensions originating from the base (Riley, 1994; Junker, Boomker & Bolton, 1999) and in *Agema* Riley, Hill & Huchzermeyer, 1997, *Sebekia* and *Pelonia* only the longer ventral extension may be present or the shorter extension ends in a smooth collar (Riley et al., 1990; Riley, Hill & Huchzermeyer, 1997). *Leiperia* Sambon, 1922 possesses an elaborate, flared cirrus-tip that is accompanied by a chitinous scoop-like structure (Riley & Huchzermeyer, 1996; Junker, Boomker, Swanepoel & Taraschewski, 2000). This characteristic sets *Leiperia* apart not only from *D. megastoma* but also from the other crocodilian and chelonian sebekiid genera.

For the above reasons we do not concur with Self & Rego's (1985) abandonment of the genus *Diesingia* and the placement of *D. megastoma* in *Sebekia*. Based on the morphological similarities between *D. megastoma* and its (South American) sebekiid counterparts, however, it is reasonable to include *Diesingia* in the family Sebekiidae, as suggested by Riley (1994).

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A check-list of the pentastomid parasites of crocodilians and freshwater chelonians

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ABSTRACT

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Based on published records and own data a summary is given of the geographical distribution of the currently known species of pentastomid parasites infecting crocodiles and alligators, as well as freshwater chelonians. A brief generic diagnosis is provided for each genus.

Fourteen out of the currently 23 living crocodilian species have been recorded as being host to one or more pentastomes. Out of the 32 pentastome species six are considered *species inquirendae*. Presently, six genera of crocodilian pentastomes, *Agema, Alofia, Leiperia, Sebekia, Selfia* and *Subtriquetra* are recognized. African crocodiles harbour eight pentastome species, six of which have been recorded from the Nile crocodile, *Crocodylus niloticus*. Three species belong to the genus *Sebekia*, *Alofia* being represented by two and *Leiperia* by only one species. Two species, *Alofia parva* and *Agema silvaepalustris*, occur in the dwarf crocodile, *Osteolaemus tetraspis*, and the slender-snouted crocodile, *Crocodylus cataphractus*, exclusively, but a single *Sebekia* species is shared with the Nile crocodile. The genus *Agema* is endemic to the African region. Infective stages of the pentastome *Subtriquetra rileyi*, thought to utilize Nile crocodiles as final hosts, have been recovered only from fishes. The largest number of pentastome species is found in the Australasian region. Of these, the Indo-Pacific crocodile, *Crocodylus porosus*, harbours seven, representing the genera *Alofia, Sebekia, Leiperia* and *Selfia*. *Selfia* is exclusive to the latter host. The genus *Subtriquetra* has been reported from "Indian crocodiles", a term possibly referring to either *Crocodylus palustris*, *Crocodylus porosus* or *Gavialis gangeticus*. Ten species of pentastomes parasitizing the crocodilian genera *Alligator*, *Caiman*, *Crocodylus* and *Melanosuchus* have been recorded from the Neotropical region including the southern states of the North American continent. The two most wide-spread pentastome genera, *Alofia* and *Sebekia*, have been recorded together with representatives of the genus *Subtriquetra* and immature and larval forms of *Leiperia.*

To date the two monospecific genera, *Pelonia*, from two terrapin species, *Pelusios sinuatus* and *Pelomedusa subrufa*, in South Africa, and *Diesingia* from *Hydraspis geoffroyana* and *Hydromedusa tectifera* in South America, are the only chelonian pentastomes recovered world-wide. A possible exception is the crocodilian pentastome *Sebekia mississippiensis* which can reach maturity in experimentally infected terrapins.

Keywords: *Agema*, *Alligator*, *Alofia*, *Caiman*, *Crocodylus*, *Diesingia*, *Gavialis*, *Hydraspis*, *Hydromedusa*, *Leiperia*, *Melanosuchus*, *Pelomedusa*, *Pelonia*, Pentastomida, *Phrynops*, *Sebekia*, *Selfia*, *Subtriquetra*, terrapins

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INTRODUCTION

The pentastomid parasites of chelonians and crocodilians are currently divided into the family Sebekidae and Subtriquetridae. The former comprises seven genera, namely, *Agema, Alofia, Selfia, Sebekia*, *Leiperia*, *Diesingia* and *Pelonia*. While the first four genera inhabit the lungs and bronchioles of the crocodilian host, *Leiperia* occurs in the trachea and bronchi (Riley, Spratt & Winch 1990; Riley 1994; Riley & Huchzermeyer 1996; Riley, Hill & Huchzermeyer 1997). *Diesingia* and *Pelonia* parasitize the lungs of chelonian final hosts (Junker & Boomker 2002; Junker, Riley & Boomker 2003).

A single member of *Sebekia, Sebekia mississippiensis*, might be able to reach maturity in chelonians, too, but as yet no mature specimens have been collected from naturally infected hosts (Dukes, Shealy & Rogers 1971). Members of the monogeneric family Subtriquetridae inhabit the nasopharynx of their crocodilian final hosts, but *Subtriquetra rileyi*, of which currently only infective larvae have been recovered, needs verification (Winch & Riley 1986a; Junker, Boomker & Booyse 1998).

During the past 10 years renewed progress has been made as regards the taxonomy of crocodilian pentastomes. The older genera, *Alofia*, *Sebekia* and *Leiperia*, have been revised, and examination of new material has led to the description of several new genera and species (Riley 1994; Riley *et al.* 1990, 1997; Riley & Huchzermeyer 1996; Junker *et al.* 1998). However, there is a dearth of data concerning the chelonian pentastomids.

In order to provide a quick reference tool, this check-list consists of two parts, following the example of Sambon (1922). The first part lists the parasites under their scientific names, their synonyms and their authorities. A short generic diagnosis precedes each genus and the parasites are grouped according to the geographic distribution of their respective hosts. The list starts with Africa, followed by Australasia. South and North America are listed last.

The second part of the check-list alphabetically lists the hosts and their synonyms, and, also in alphabetical order, their respective parasites. The nomenclature and synonyms of the crocodilian and chelonian hosts are according to Getz (2002).

Only references dealing with mature pentastomes are included in the check-list, but for completeness' sake the intermediate hosts of pentastome species of which only larval forms are known are listed.

PARASITE/HOST CHECK-LIST OF THE PENTASTOMIDA

FAMILY SEBEKIDAE SAMBON, 1922

Genus *Agema* Riley, Hill & Huchzermeyer, 1997

GENERIC DIAGNOSIS: Overall shape typical of smaller members of the Sebekidae; males claviform, females with more uniform diameter and conical posterior terminating in a small blunt point; adult hooks smooth; blades smoothly curved without abrupt right-angled bend near to base; blade on anterior hook pair larger than that of posterior pair; fulcrum without cowl; mouth ovoid and sides of cadre united anteriorly and posteriorly by segments of chitin which appear as two crescents; copulatory spicules delicate and elongate; basal section without a hooked collar (Riley *et al.* 1997).

AFRICA

1. *Agema silvaepalustris* Riley, Hill & Huchzermeyer, 1997

    Crocodylus cataphractus

        Riley, Hill & Huchzermeyer (1997), Republic of the Congo

    Osteolaemus tetraspis

        Riley, Hill & Huchzermeyer (1997), Republic of the Congo

Genus *Alofia* Giglioli, 1922

GENERIC DIAGNOSIS: Size small; body banana-shaped; hooks large with long, narrow, slightly curved blade and a slender base; absence of chitinous formation at the base of the anterior hook; chitinous buccal cadre large and U-shaped; intestine as in *Sebekia*; found in crocodiles (Fain 1961 in Riley 1994); caudal extremity of female bluntly rounded, often swollen into a bulb (Riley 1994); hooks usually smooth (rarely with patches of minute spines [see *Alofia nilotici* and *Alofia parva* (Riley & Huchzermeyer 1995a, b)], blades finely canaliculated, bent through almost a right angle at the base; peg-like extension of oral cadre projects into oesophagus; copulatory spicules with double-hooked collar on the shorter of the two anterior extensions (Riley & Huchzermeyer 1995a, b; Junker, Boomker & Bolton 1999).

AFRICA

1. *Alofia nilotici* Riley & Huchzermeyer, 1995

    Crocodylus niloticus

Riley & Huchzermeyer (1995a), Botswana

Junker, Boomker & Bolton (1999), South Africa

2. *Alofia parva* Riley & Huchzermeyer, 1995

Crocodylus cataphractus

Riley & Huchzermeyer (1995b, 2000), Republic of the Congo

Osteolaemus tetraspis osborni

Riley & Huchzermeyer (1995b, 2000), Republic of the Congo

3. *Alofia simpsoni* Riley, 1994

Unknown crocodilian

Riley (1994), Ghana

Crocodylus niloticus

Riley & Huchzermeyer (1995a), Botswana

Junker, Boomker & Bolton (1999), South Africa

AUSTRALASIAN REGION

4. *Alofia ginae* Giglioli, 1922

Unknown crocodilian

Sambon (1922), Samoa

Most probably *Crocodylus porosus*, as it is the only crocodilian whose range extends as far as Fiji in the Pacific Ocean and it is known to have colonized many small islands as far as nearly 1 000 km from land (Ross 1989).

Crocodylus porosus (?)

Riley (1994), Philippines

The collector did not specify the host, but Riley (1994) concludes it to be *C. porosus*, as the only other Philippinian crocodile, *Crocodylus mindorensis*, does not occur in the region from which the parasites were recovered.

5. *Alofia merki* Giglioli, 1922

Sebekia merki Heymons, 1941

Unknown crocodilian

Sambon (1922), Samoa

Most probably *Crocodylus porosus*, as it is the only crocodilian whose range extends as far as Fiji in the Pacific Ocean and it is known to have colonized many small islands as far as nearly 1 000 km from land (Ross 1989).

Crocodylus porosus

Riley (1994), Northern Territory, Australia

Riley (1994), Philippines

6. *Alofia indica* (Von Linstow, 1906) Hett, 1924, *species inquirenda*

Gavialis gangeticus

Hett (1924), India

SOUTH & NORTH AMERICAN REGION

7. *Alofia platycephala* (Lohrmann, 1889) Giglioli, 1922

Pentastomum platycephalum Lohrmann, 1889; *Porocephalus platycephalus* Shipley, 1898; *Reighardia platycephala* Sambon, 1910

Unknown crocodilian

Lohrmann (1889), South America

Caiman crocodilus

Self & Rego (1985), Brazil

Caiman latirostris

Heymons (1941), Paraguay

Comment: Hirst (1922) described *Alofia adriatica* (Hirst, 1922) Giglioli, 1922 from an unknown host from the Adriatic. As crocodilians do not occur in the Adriatic this species will have to remain *species inquirenda* until further material becomes available.

Genus *Leiperia* Sambon, 1922

GENERIC DIAGNOSIS: Female with spirally coiled abdomen; broad bands of chloride cells; hooks smooth, flat-topped with sharply curved blade; oral cadre V-shaped with large anterior flanges, numerous pores around the pharynx; copulatory spicules heavily chitinized with complex internal supporting structures, shorter of the two anterior extensions forms a smooth collar (double in *L. australiensis*) around the longer spatulate extension; cirrus tip modified into a flattened trumpet of longitudinally-striated chitin (Riley & Huchzermeyer 1996; Junker, Boomker, Swanepoel & Taraschewski 2000).

AFRICA

1. *Leiperia cincinnalis* (Vaney & Sambon, 1910) Sambon, 1922

Reighardia cincinnalis Vaney & Sambon, 1910;

Porocephalus nematoides De Beauchamp, 1918

Crocodylus cataphractus

Fain (1961), Central Africa: infective larva

Crocodylus niloticus

Vaney & Sambon (1910), Uganda

Sambon (1922), Zimbabwe

Rodhain & Vuylsteke (1932), Democratic Republic of the Congo

Junker, Boomker, Swanepoel & Taraschewski (2000), South Africa

AUSTRALASIAN REGION

2. *Leiperia australiensis* Riley & Huchzermeyer, 1996

Crocodylus johnsoni

Riley & Huchzermeyer (1996), Northern Territory, Australia

Crocodylus porosus

Riley & Huchzermeyer (1996), Northern Territory, Australia

SOUTH & NORTH AMERICAN REGION

3. *Leiperia gracilis* Diesing, 1936, *species inquirenda*

Pentastoma gracile Diesing, 1836 (*partim*); *Pentastomum gracile* Leidy, 1856; *Pentastoma gracilis* Parona, 1891; *Porocephalus gracilis* Shipley, 1898; *Porocephalus crocodili* Wheeler, 1915 (*partim*); *Leiperia neotropica* Heymons & Vitzthum, 1935

Immature and larval forms were recovered from the following hosts, but adults have not been collected.

Alligator mississippiensis

Leidy (1856, in Sambon 1922), locality unknown, North America

Crocodylus acutus

Heymons (1935), South America

Caiman crocodilus

Heymons (1935), Brazil

Genus *Sebekia* Sambon, 1922

GENERIC DIAGNOSIS: Body short and squat with 58–94 compressed annuli; lateral lines conspicuous; cephalothorax small, wedge-shaped and projecting nipple-like from the abdomen, ventral surface continuous with that of the abdomen; mouth subterminal and shaped like an inverted 'U'; oral cadre oval to elongate, highly variable in shape, without long, parallel sides and generally united anteriorly; hooks small, equal or subequal, claw-shaped, with convex or flat dorsal surface; all hooks spiny (rarely only the anterior pair); all fulcra often with spinous anterior extension (rarely only the anterior pair); hook barb curved, strongly united and continuous with shank; spicules generally obpyriform, with one or two fine sclerotized rods supporting membranous region distally. Parasites of the lungs of crocodilians, rarely of chelonians (Riley *et al.* 1990).

AFRICA

1. *Sebekia cesarisi* Giglioli, 1922

Crocodylus sp.

Sambon (1922), Africa

Crocodylus niloticus

Riley & Huchzermeyer (1995a), Botswana

Junker, Boomker & Bolton (1999), South Africa

2. *Sebekia okavangoensis* Riley & Huchzermeyer, 1995

Sebekia cesarisi Riley, Spratt & Winch, 1990

Crocodylus cataphractus

Riley & Huchzermeyer (2000), Republic of the Congo

Crocodylus niloticus

Riley & Huchzermeyer (1995a), Botswana

Junker, Boomker & Bolton (1999), South Africa

Osteolaemus tetraspis

Riley & Huchzermeyer (2000), Republic of the Congo

3. *Sebekia wedli* Giglioli, 1922

Pentastoma oxycephalum var. *minor* Wedli, 1861; *Sebekia oxycephala* Self & Rego, 1985

Crocodylus niloticus

Devos (1939), Democratic Republic of the Congo

Riley, Spratt & Winch (1990), Uganda

Riley & Huchzermeyer (1995a), Botswana

Junker, Boomker & Bolton (1999), South Africa

AUSTRALASIAN REGION

4. *Sebekia johnstoni* Riley, Spratt & Winch, 1990

Crocodylus johnsoni

Riley, Spratt & Winch (1990), Northern Territory, Australia

Crocodylus porosus

Riley, Spratt & Winch (1990), Northern Territory, Australia

5. *Sebekia multiannulata* Riley, Spratt & Winch, 1990

Crocodylus johnsoni

Riley, Spratt & Winch (1990), Northern Territory, Australia

Crocodylus porosus

Riley, Spratt & Winch (1990), Northern Territory, Australia

6. *Sebekia purdieae* Riley, Spratt & Winch, 1990

Crocodylus porosus

Riley, Spratt & Winch (1990), Northern Territory, Australia

7. *Sebekia jubini* (Vaney & Sambon, 1910) Sambon, 1922, *species inquirenda*

Porocephalus jubini Vaney & Sambon, 1910

Crocodylus siamensis

Sambon (1922), locality unknown, southeast Asia

8. *Sebekia novaeguineae* Riley, Spratt & Winch, 1990

Crocodylus novaeguineae

Riley, Spratt & Winch (1990), Papua New Guinea

SOUTH & NORTH AMERICAN REGION

9. *Sebekia acuminata* Travassos, 1924, *species inquirenda*

Unknown crocodilian

Travassos (1924), Brazil

10. *Sebekia divestei* Giglioli, 1922

Crocodylus acutus

Sambon (1922), locality unknown, Neotropical region

11. *Sebekia microhamus* Self & Rego, 1985

Caiman crocodilus

Self & Rego (1985), Brazil

12. *Sebekia mississippiensis* Overstreet, Self & Vliet, 1985

Pentastoma oxycephalum Diesing, 1836 (*partim*); *Pentastomum gracile* (syn. *Leiperia gracilis*) Leidy, 1856

Alligator mississippiensis

Deakins (1971), USA

Hazen, Aho, Murphy, Esch & Schmidt (1978), USA

Overstreet, Self & Vliet (1985), USA

13. *Sebekia oxycephala* (Diesing, 1836) Sambon, 1922

Pentastoma proboscideum Rudolphi, 1819 (*partim*); *Pentastoma oxycephalum* Diesing, 1836 (*partim*); *Pentastoma gracile* Diesing, 1836 (*partim*); *Pentastomum oxycephalum* Diesing, 1850 (*partim*); *Pentastomum gracile* Diesing, 1850 (*partim*); *Pentastomum heterodontis* Leuckart, 1860; *Pentastomum oxycephalum* Chatin, 1882; *Porocephalus oxycephalus* Stiles, 1893; *Pentastoma proboscideum crocodili sclerops* Rudolphi (Shipley in Sambon 1922); *Reighardia oxycephala* Vaney & Sambon, 1910; *Porocephalus crocodili* Wheeler, 1913 (*partim*); *Sebekia oxycephala* Sambon, 1922 (*partim*); *Bdukus ichthyius* Holl, 1929; *Leiperia heterodontis* Heymons & Vitzthum, 1935; *Sebekia crocodili* Heymons & Vitzthum, 1935

Alligator mississippiensis

Sambon (1922), locality unknown

Caiman crocodilus

Sambon (1922), locality unknown

Winch & Riley (1986b), Trinidad, South America

Caiman latirostris

Heymons (1941), locality unknown

Crocodylus acutus

Sambon (1922), locality unknown

14. *Sebekia samboni* Travassos, 1924, *species inquirenda*

Unknown crocodilian

Travassos (1924), Brazil

15. *Sebekia trinitatis* Riley, Spratt & Winch, 1990

Caiman crocodilus

Riley, Spratt & Winch (1990), Trinidad, South America

Genus *Selfia* Riley, 1994

GENERIC DIAGNOSIS: Size small, cephalothorax minute in comparison with diameter of the abdomen; 78–82 well defined annuli; abdomen strongly curled ventrally; caudal extremity of female abruptly tapered to blunt point; hooks very small, with tiny blade only slightly offset from transversely creased and folded shank; rear of anterior hooks enveloped by soft, spinous cowl which forms an extension of the fulcrum; buccal cadre somewhat variable in shape, being oval to more U-shaped, but lacking parallel sides; copulatory spicule of male like that of *Alofia* (Riley 1994).

AUSTRALASIAN REGION

1. *Selfia porosus* Riley, 1994

Crocodylus porosus

Riley (1994), Northern Territory, Australia

Genus *Diesingia* Sambon, 1922

GENERIC DIAGNOSIS: Hooks smooth, flat-topped, with sharply curved blades; fulcra with anterior cowl-like extension, extension smooth in posterior and spiny in anterior fulcra; oral cadre open anteriorly with an oesphageal peg similar to that in *Alofia*; copulatory spicule with cowry shell-shaped base, the short, ventral extension is transformed into a structure resembling the collembolan fulcrum, and is connected to the base by a joint (Junker, Riley & Boomker 2003).

SOUTH & NORTH AMERICAN REGION

1. *Diesingia megastoma* (Diesing, 1836) Sambon, 1922

Pentastoma megastomum Diesing, 1836; *Pentastomum megastomum* Leuckart, 1860; *Porocephalus megastomus* Shipley, 1898; *Sebekia megastoma* Travassos, 1923; *Sebekia crocodili* Heymons & Vitzthum, 1935; *Diesingia megastoma* Heymons; 1941; *Butantanella megastoma* Da Fonseca & Ruiz, 1956; *Sebekia megastoma* Self & Rego, 1985

Phrynops geoffroanus

Diesing (1836), Brazil

Hydromedusa tectifera

Da Fonseca & Ruiz (1956), Brazil

Genus *Pelonia* Junker & Boomker, 2002

GENERIC DIAGNOSIS: Hooks smooth, dorsally convex, with sharply bent blades, fulcra without extensions; oral cadre more or less U-shaped, closed anteriorly by delicate chitinous fibres; copulatory spicules almost identical to those of *Sebekia wedli*, with cowry shell-shaped base and the short anterior extension ending in a smooth collar, the long spatulate extension carries small chitinous teeth (Junker & Boomker 2002).

AFRICA

1. *Pelonia africana* Junker & Boomker, 2002

Pelomedusa subrufa

Junker & Boomker (2002), South Africa

Pelusios sinuatus

Junker & Boomker (2002), South Africa

FAMILY SUBTRIQUETRIDAE FAIN, 1961

Genus *Subtriquetra* Sambon, 1922

GENERIC DIAGNOSIS: Body elliptical, ventrally flattened and dorsally dome shaped with flattened margins; hooks simple, slender and sharply pointed, disposed in a curved line; oral cadre rounded (Fain 1961; Winch & Riley 1986a; Junker *et al.* 1998).

AFRICA

1. *Subtriquetra rileyi* Junker, Boomker & Booyse, 1998

Infective larvae:

Tilapia rendalli swierstrae

Junker, Boomker & Booyse (1998), South Africa

Oreochromis mossambicus

Junker, Boomker & Booyse (1998), South Africa

AUSTRALASIAN REGION

2. *Subtriquetra megacephala* (Baird, 1853) Sambon, 1922

Pentastoma megacephalum Baird, 1853; *Porocephalus megacephalus* Shipley, 1898

Crocodylus palustris

Sambon (1922), Sunderbunds, India

Crocodylus palustris, *Crocodylus porosus* or

Gavialis gangeticus? ("Sangor crocodile")

Sambon (1922), Bengal, India

3. *Subtriquetra shipleyi* Hett, 1924

Crocodylus palustris Crocodylus porosus or *Gavialis gangeticus* ? ("Indian crocodile")

Hett (1924), India

SOUTH & NORTH AMERICAN REGION

4. *Subtriquetra subtriquetra* (Diesing, 1836)

Pentastoma proboscideum Bresmer, 1824 (*partim*); *Pentastoma subtriquetrum* Diesing, 1836; *Pentastomum subtriquetrum* Diesing, 1850; *Pentastomum pusillum* Diesing, 1856; *Linguatula subtriquetra* Raillet, 1883; *Linguatula pusilla* Shipley, 1898

Caiman crocodilus

Sambon (1922), South America

Winch & Riley (1986a), Trinidad, South America

Melanosuchus niger

Sambon (1922), South America

HOST/PARASITE CHECK-LIST OF THE PENTASTOMIDA

Crocodylia

FAMILY ALLIGATORIDAE (CUVIER, 1807) (Alligators and caimans)

Genus *Alligator* Cuvier, 1807

1. *Alligator mississippiensis* (Daudin, 1801) Daudin, 1802 (American alligator)

Crocodilus mississipiensis Daudin, 1801

Leiperia gracilis, species inquirenda, larval forms only

Sebekia mississippiensis

Sebekia oxycephala

Genus *Caiman* Spix, 1825

1. *Caiman crocodilus* (Linnaeus, 1758) (Common or Spectacled caiman)

Lacerta crocodilus Linnaeus, 1758; *Caiman sclerops* Schneider, 1801 (fide Medem 1981); *Perosuchus fuscus* Cope, 1868; *Alligator* (*Jacare*) *chiapasius* Bocourt, 1876

Alofia platycephala

Leiperia gracilis, species inquirenda, larval forms

Sebekia microhamus

Sebekia oxycephala

Sebekia trinitatis

Subtriquetra subtriquetra

2. *Caiman latirostris* (Daudin, 1801) (Broad-snouted caiman)

Crocodilus latirostris Daudin, 1801; *Caiman fissipes* Spix, 1825; *Champsa fissipes* Wagler, 1828 (*fide* Hoogmoed & Gruber, 1983); *Alligator cynocephalus* Duméril & Bibron, 1836; *Jacare latirostris* Gray, 1862; *Alligator latirostris* Boulanger, 1886; *Jacaretinga latirostris* Vaillant, 1898

Alofia platycephala

Sebekia oxycephala

Genus *Melanosuchus* Gray, 1862

1. *Melanosuchus niger* (Spix, 1825) (Black caiman)

Caiman niger Spix, 1825

Subtriquetra subtriquetra

FAMILY CROCODYLIDAE (CUVIER, 1807) (Crocodiles)

SUBFAMILY CROCODYLINAE (CUVIER, 1807)

Genus *Crocodylus* Laurenti, 1768

1. *Crocodylus acutus* (Cuvier, 1807) (American crocodile)

Crocodilus acutus Cuvier, 1807

Leiperia gracilis, species inquirenda, larval forms only

Sebekia divestei

Sebekia oxycephala

2. *Crocodylus cataphractus* Cuvier, 1825 (Slender-snouted crocodile)

Crocodilus cataphractus Falconer, 1846

Agema silvaepalustris

Alofia parva

Leiperia cincinnalis, infective larva

Sebekia okavangoensis

3. *Crocodylus johnsoni* Krefft, 1873 (Australian freshwater crocodile)

   Tomistoma kreffti Gray in Krefft, 1873 (*nomen nudum*); *Crocodilus* (*Philas*) *johnstoni* Gray, 1874; *Crocodylus johnstoni* Cogger, 2000

   - *Leiperia australiensis*
   - *Sebekia johnstoni*
   - *Sebekia multiannulata*

4. *Crocodylus niloticus* Laurenti, 1768 (Nile crocodile)

   Crocodilus vulgaris Cuvier, 1807; *Crocodilus multiscutatus* Rüppell in Cretzschmar, 1826; *Crocodilus marginatus* Geoffroy, 1827; *Crocodilus madagascariensis* Grandidier, 1872; *Crocodilus vulgaris* var. *madagascariensis* Boettger, 1877

   - *Alofia nilotici*
   - *Alofia simpsoni*
   - *Leiperia cincinnalis*
   - *Sebekia cesarisi*
   - *Sebekia okavangoensis*
   - *Sebekia wedli*

5. *Crocodylus novaeguineae* Schmidt, 1928 (New Guinea crocodile)

   - *Sebekia novaeguineae*

6. *Crocodylus palustris* Lesson, 1831 (Mugger, Marsh crocodile)

   - *Subtriquetra megacephala*
   - *Subtriquetra shipleyi* ("Indian crocodile")

7. *Crocodylus porosus* Schneider, 1801 (Indo-Pacific or Saltwater crocodile)

   Crocodylus natans Meyer, 1795; *Crocodilus porosus* Schneider, 1801; *Crocodilus oopholis* Schneider, 1801; *Crocodilus biporcatus* Cuvier, 1807; *Crocodilus biporcatus raninus* Müller & Schlegel, 1844; *Oopholis pondicherianus* Gray, 1862; *Crocodylus porosus australis* Deraniyagala, 1953; *Crocodylus porosus minikanna* Deraniyagala, 1953

   - *Alofia ginae* (possibly *Crocodylus mindorensis*, but distributionally unlikely)
   - *Alofia merki*
   - *Leiperia australiensis*
   - *Sebekia johnstoni*
   - *Sebekia multiannulata*
   - *Sebekia purdieae*
   - *Selfia porosus*
   - *Subtriquetra shipleyi* ("Indian crocodile")

8. *Crocodylus siamensis* Schneider, 1801 (Siamese crocodile)

   Crocodilus galeatus Cuvier, 1807

   - *Sebekia jubini*, species *inquirenda*

Genus *Osteolaemus* Cope, 1861

1. *Osteolaemus tetraspis* Cope, 1861 (Dwarf crocodile)

   Crocodilus frontatus Murray, 1862; *Halcrosia afzelii* Lilljeborg, 1867; *Halcrosia nigra* Gray, 1867; *Halcrosia nigra* Gray, 1870; *Osteoblepharon osborni* Schmidt, 1919; *Osteolaemus tetraspis tetraspis* Wermuth & Mertens, 1961

   - *Agema silvaepalustris*
   - *Alofia parva*
   - *Sebekia okavangoensis*

FAMILY GAVIALIDAE ADAMS, 1854 (Gharials)

Genus Gavialis Oppel, 1811

1. *Gavialis gangeticus* (Gmelin, 1789) (Gharial)

   Lacerta gangetica Gmelin, 1789

   - *Subtriquetra megacephala* ("Indian crocodile")
   - *Subtriquetra shipleyi* ("Indian crocodile")

CHELONIA

Suborder Pleurodira (Side-necked turtles)

FAMILY PELOMEDUSIDAE COPE, 1868

Genus *Pelomedusa* Wagler, 1830

1. *Pelomedusa subrufa* (Lacépède, 1788) (Cape terrapin)

   Testudo subrufa Lacépède, 1788; *Testudo galeata* Schoepff, 1792; *Testudo badia* Donndorf, 1798; *Testudo rubicunda* Suckow, 1798; *Emys olivacea* Schweigger, 1812 (*non Emys olivacea* Gray, 1855); *Pentonyx capensis* Duméril & Bibron, 1835; *Pentonyx gehafie* Rüppell, 1835; *Pentonix americana* Cornalia, 1849; *Pelomedusa mozambica* Peters (*nomen nudum*) in Gray 1855 (?); *Pelomedusa mossambicensis* Peters (*nomen nudum*) in Lichtenstein 1856; *Pelomedusa* *nigra* Gray, 1863; *Pelomedusa gasconi* Rochebrune, 1884; *Pelomedusa galeata* Boulanger, 1889; *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910; *Pelomedusa galeata orangensis* Hewitt, 1935; *Pelomedusa galeata devilliersi* Hewitt, 1935; *Pelomedusa galeata damarensis* Hewitt, 1935; *Pelomedusa subrufa wettsteini* Mertens, 1937; *Testudo emys arabica* N.-Ehrenberg in Stresemann 1954

Pelonia africana

Genus *Pelusios* Wagler, 1830

1. *Pelusios sinuatus* (Smith, 1838) (Serrated hinged terrapin, African serrated mud turtle)

   Sternotherus sinuatus Smith, 1838; *Sternotherus dentatus* Peters, 1848 (*nomen nudum*); *Sternothaerus sinuatus* Boulanger, 1889; *Sternothaerus bottegi* Boulanger, 1895; *Pelusios sinuatus zuluensis* Hewitt, 1927; *Pelusios sinuatus leptus* Hewitt, 1927

   Pelonia africana

FAMILY CHELIDAE GRAY, 1825 (Snake-necked turtles)

Genus *Hydromedusa* Wagler, 1830

1. *Hydromedusa tectifera* Cope, 1869 [1870] (South American snake-necked turtle, Uruguay snake-necked turtle)

   Hydromedusa platanensis Gray, 1873; *Hydromedusa wagleri* Günther, 1884

   Diesingia megastoma

Genus *Phrynops* Wagler, 1830

1. *Phrynops geoffroanus* (Schweigger, 1812) Gorzula & Señaris, 1999 (Geoffroy's side-necked turtle)

   Emys geoffroana Schweigger, 1812; *Emys geoffreana* Schweigger, 1812 (fide Boulanger, 1886); *Emys depressa* Merrem, 1820 (*non Emys depressa* Spix, 1824); *Emys viridis* Spix, 1824 (?); *Emys geoffroyana* Gray, 1831; *Platemys geoffreana* Duméril & Bibron, 1835; *Platemys neuwiedii* Duméril & Bibron, 1835; *Platemys waglerii* Duméril & Bibron, 1835; *Platemys tuberosa* Peters, 1870; *Platemys geoffroyana* Boulanger, 1886; *Hydraspis geoffroyana* Boulanger, 1889; *Hydraspis wagleri* Boulanger, 1889; *Hydraspis tuberosa* Boulanger, 1889; *Hydraspis boulangeri* Bohls, 1895; *Phrynops geoffroana* Mertens *et al.*, 1934; *Phrynops geoffroana geoffroana* Müller, 1939; *Phrynops tuberosa* Mertens *et al.*, 1934; *Phrynops geoffroana tuberosa* Müller, 1939

   Diesingia megastoma

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