



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

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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 margaritifera*, Hering-Hagenbeck, 2001 from the skink, *Mabuya margaritifera*, *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 re-described.

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 margaritifera*. 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 (Burse, 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 biogeog-

raphy 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 where 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 pre-

cloacal, 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 bulb. 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 bulb 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 bulb 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.

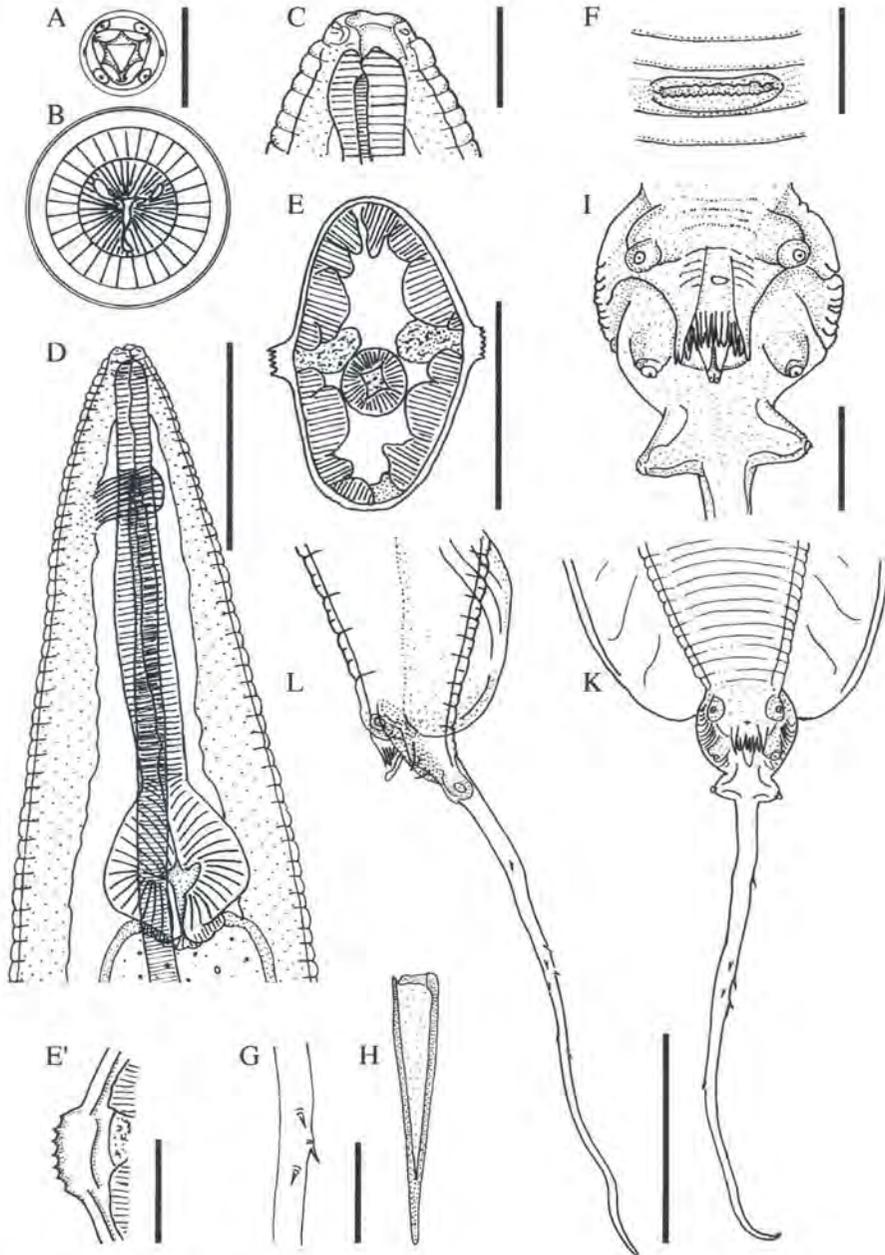


FIG. 1 *Spauligodon molopoensis*, paratype male

- 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

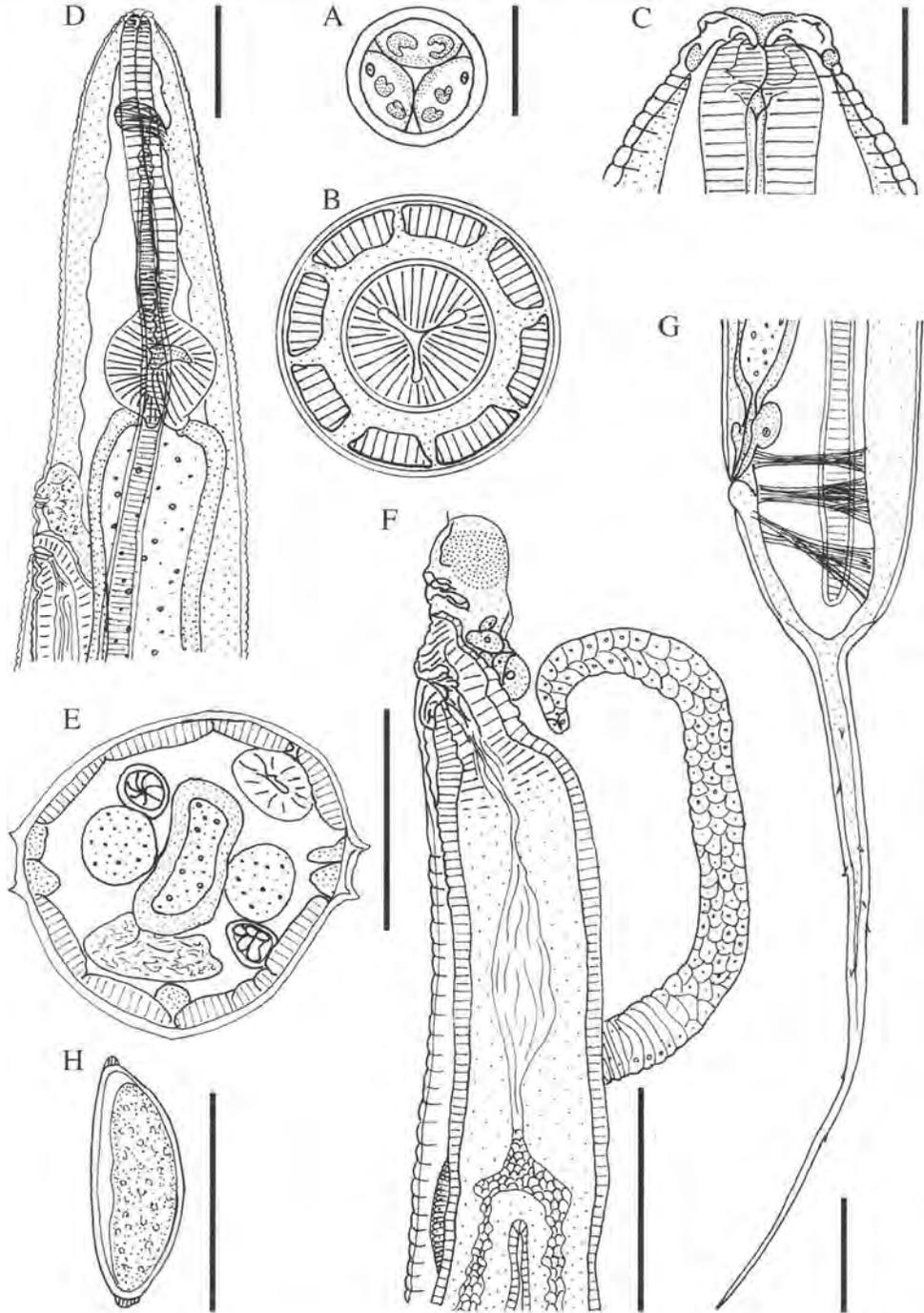


FIG. 2 *Spauligodon molopoensis*, paratype female

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

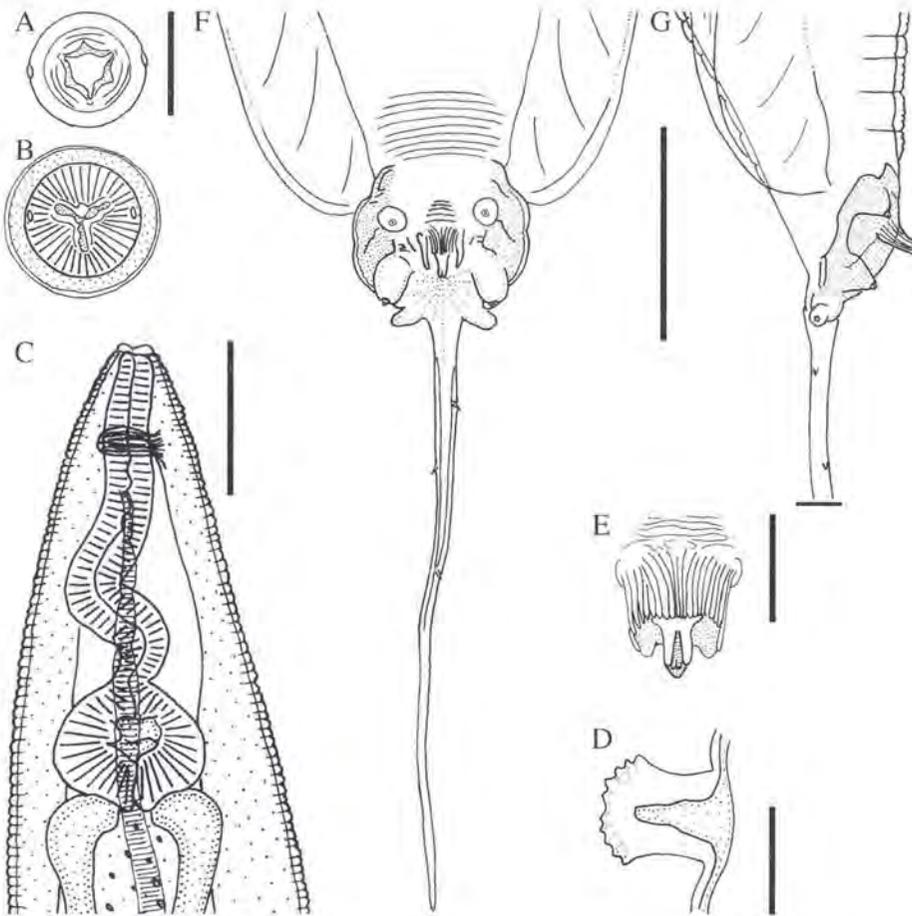


FIG. 3 *Spauligodon blydeensis*, paratype male

- 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

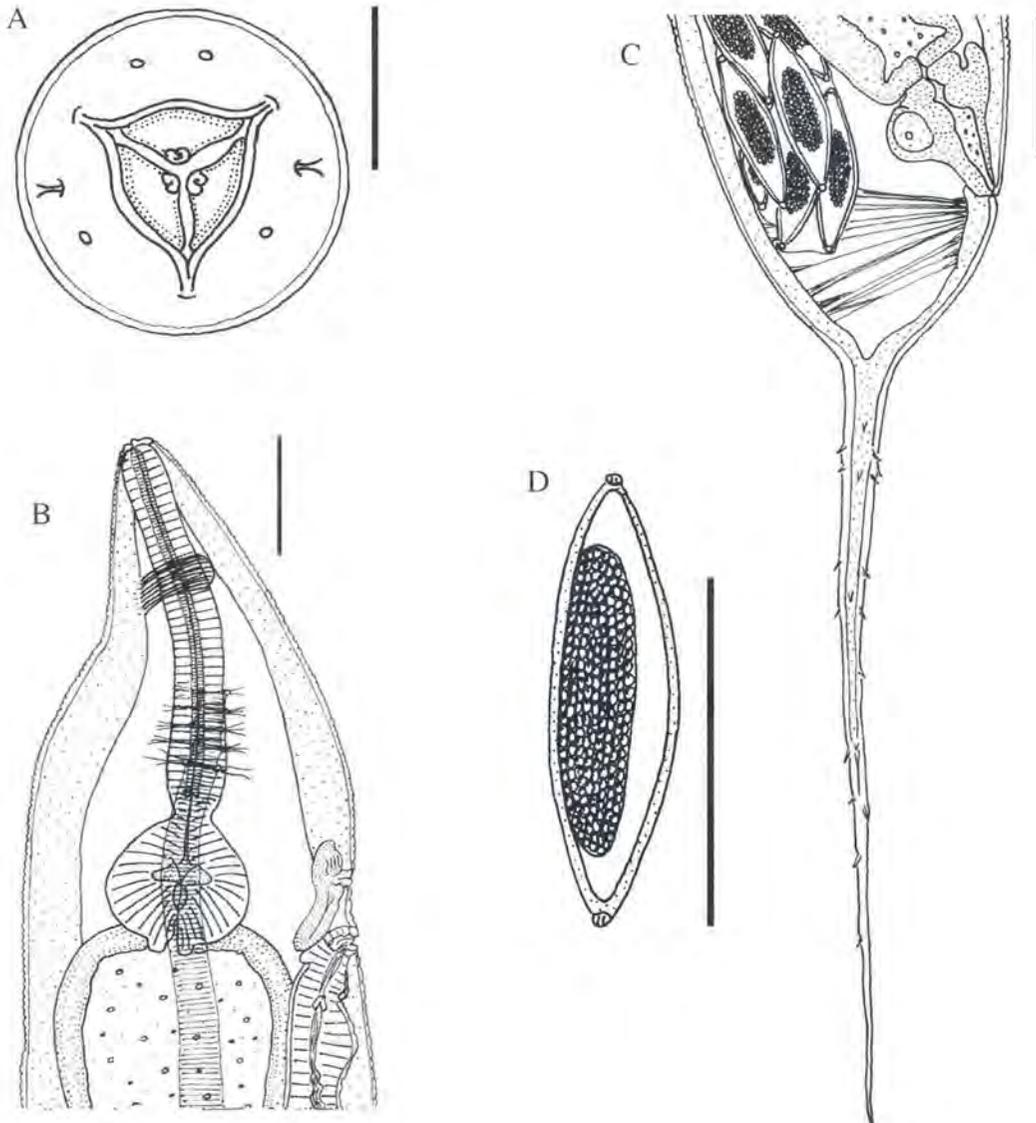


FIG. 4 *Spauligodon blydeensis*, female

- 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* Skrja-

bin, 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	<i>Spauligodon petersi</i>	<i>Spauligodon morgani</i>	<i>Spauligodon dimorpha</i>	<i>Spauligodon smithi</i>	<i>Spauligodon timbavatiensis</i>	<i>Spauligodon moloipoensis</i>	<i>Spauligodon blydeensis</i>
Author	Bursey <i>et al.</i> 1997	Fitzsimmons 1961	Chabaud & Brygoo 1962	Bursey <i>et al.</i> 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	<i>Mabuya sulcata sulcata</i>	<i>Mabuya striata</i>	<i>Chamaeleo pardalis</i>	<i>Pachydactylus bibronii</i>	<i>Pachydactylus turneri</i>	<i>Pachydactylus capensis</i>	<i>Homopholis wahlbergii</i>
Country	South Africa	Malawi	Madagascar	South Africa	South Africa	South Africa	South Africa

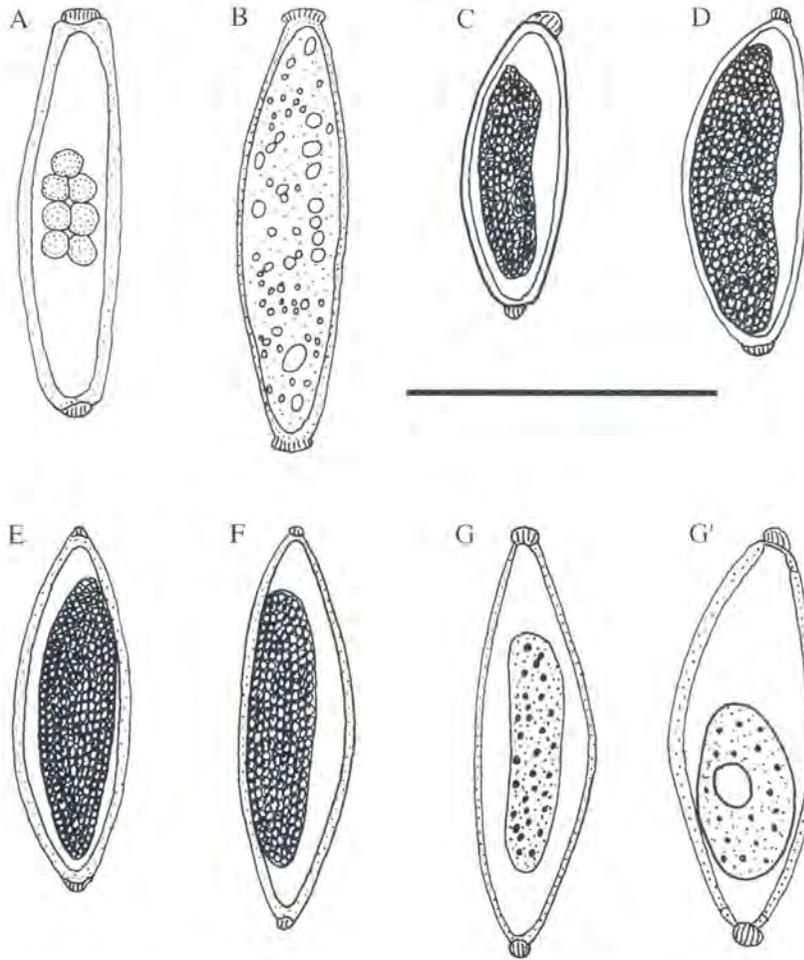


FIG. 5 Eggs of the *Spauligodon* species occurring in reptiles in the Ethiopian region.

- 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

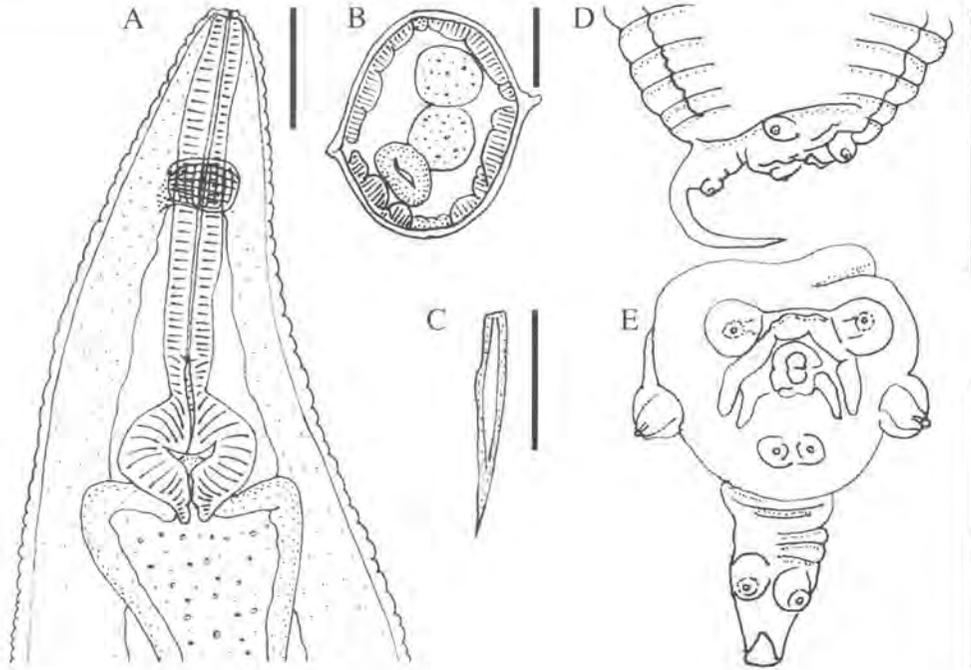


FIG. 6 *Parapharyngodon margaritiferi*, male

- 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

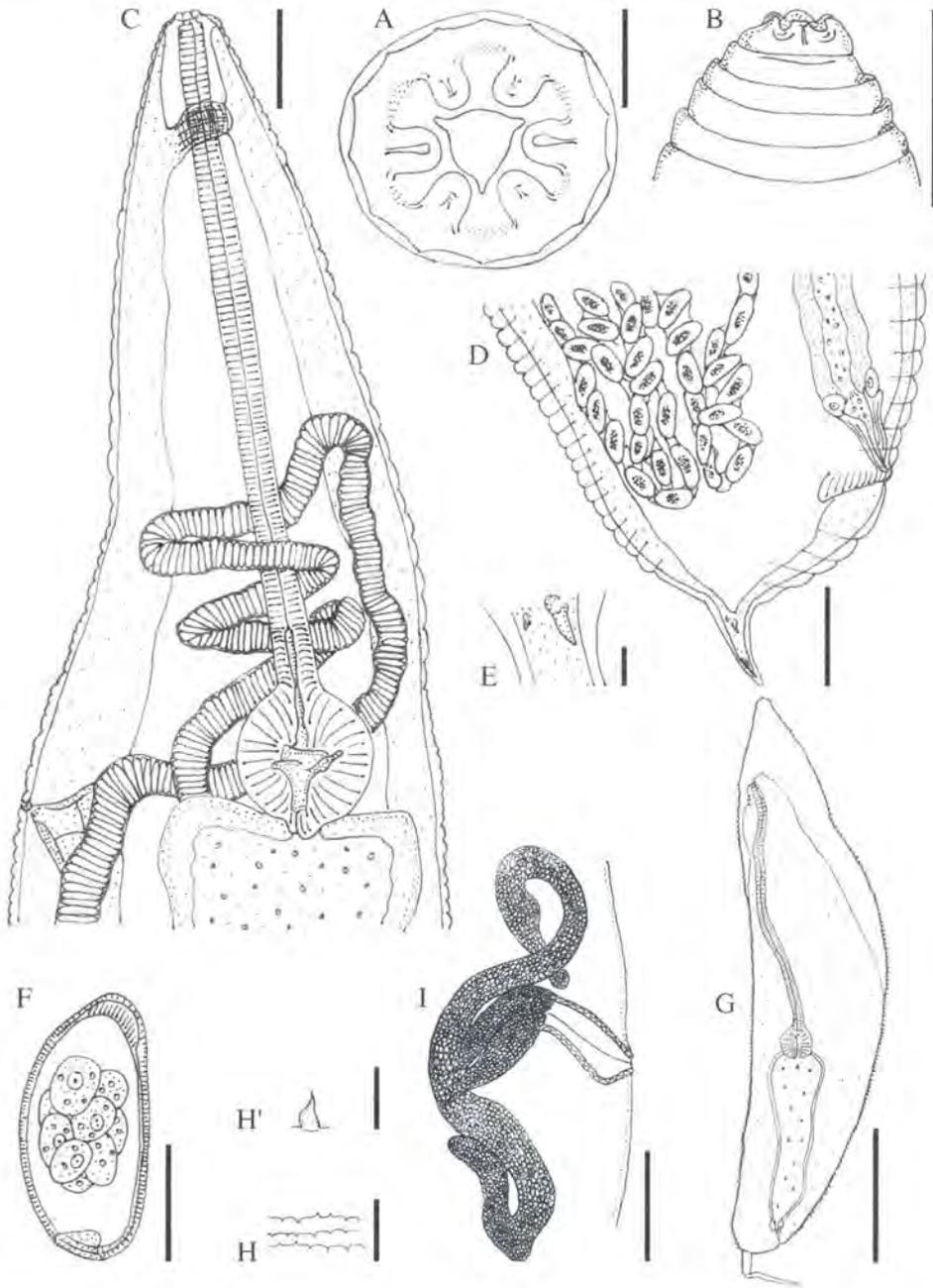


FIG. 7 *Parapharyngodon margaritiferi* female and *Pharyngodon* sp. larva

- 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

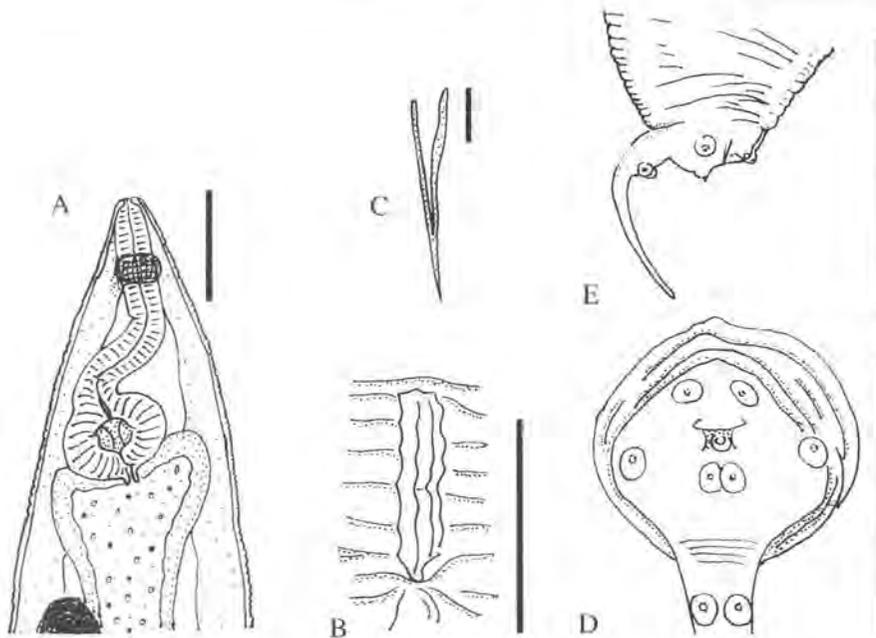


FIG. 8 *Parapharyngodon* sp. no. 1, holotype male

- 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 mid-body. 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 divi-

sion 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 mid-body. 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. margaritifera*. The worm is

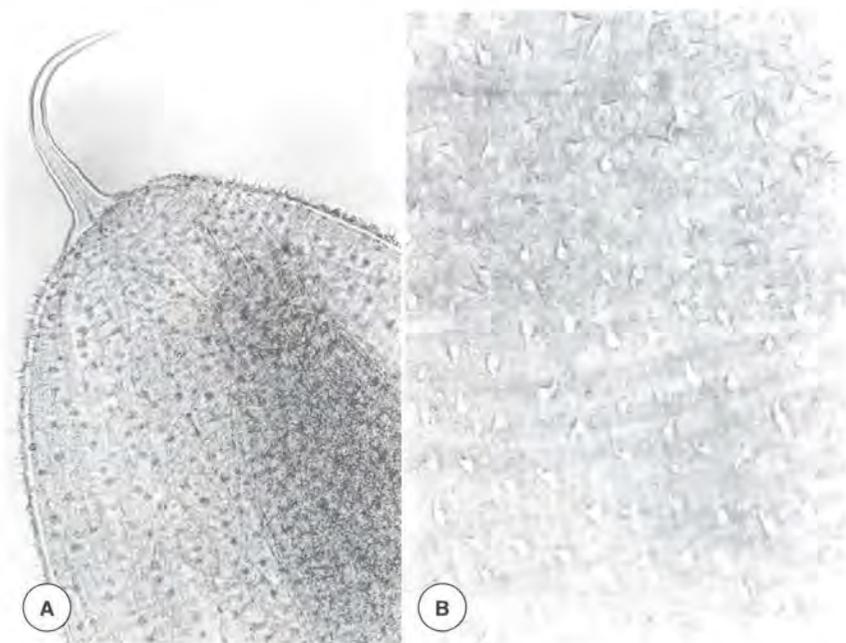


FIG. 9 *Parapharyngodon* spp. third stage larva

- 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-

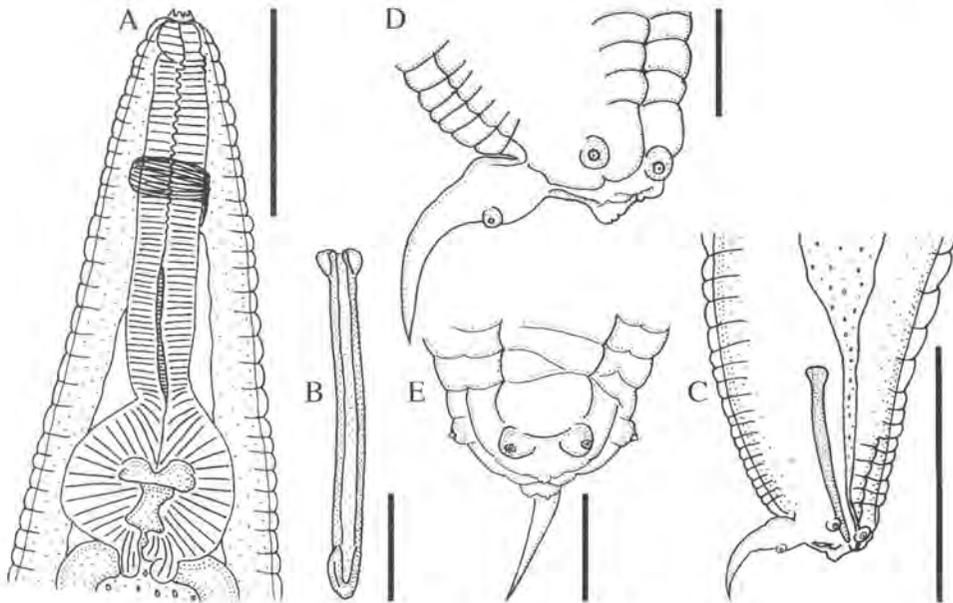


FIG. 10 *Parapharyngodon gerrhosauri*, holotype male

- 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

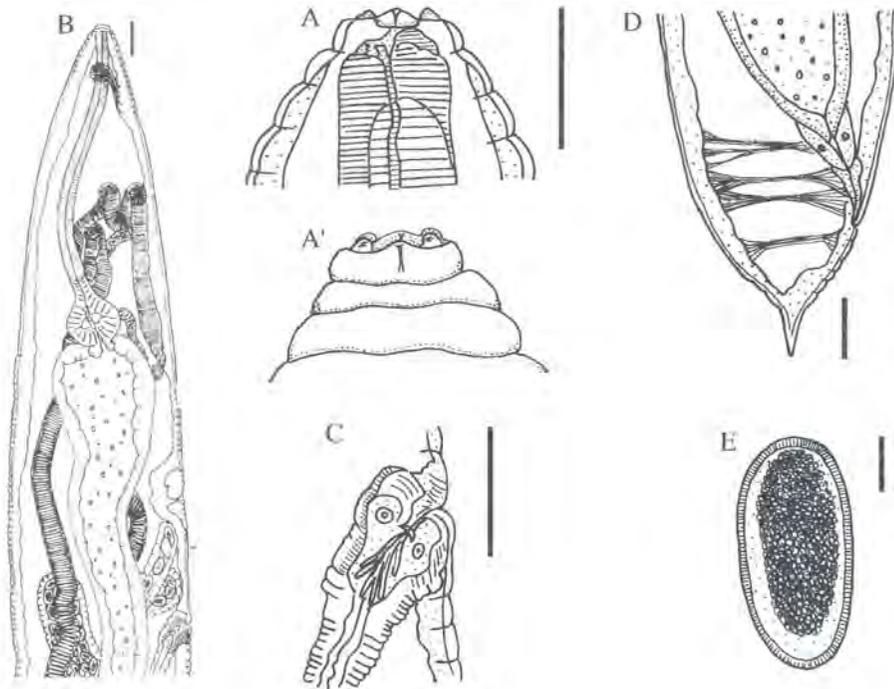


FIG. 11 *Parapharyngodon* sp. no. 3, female

- 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 bulbous 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 bulbous. 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

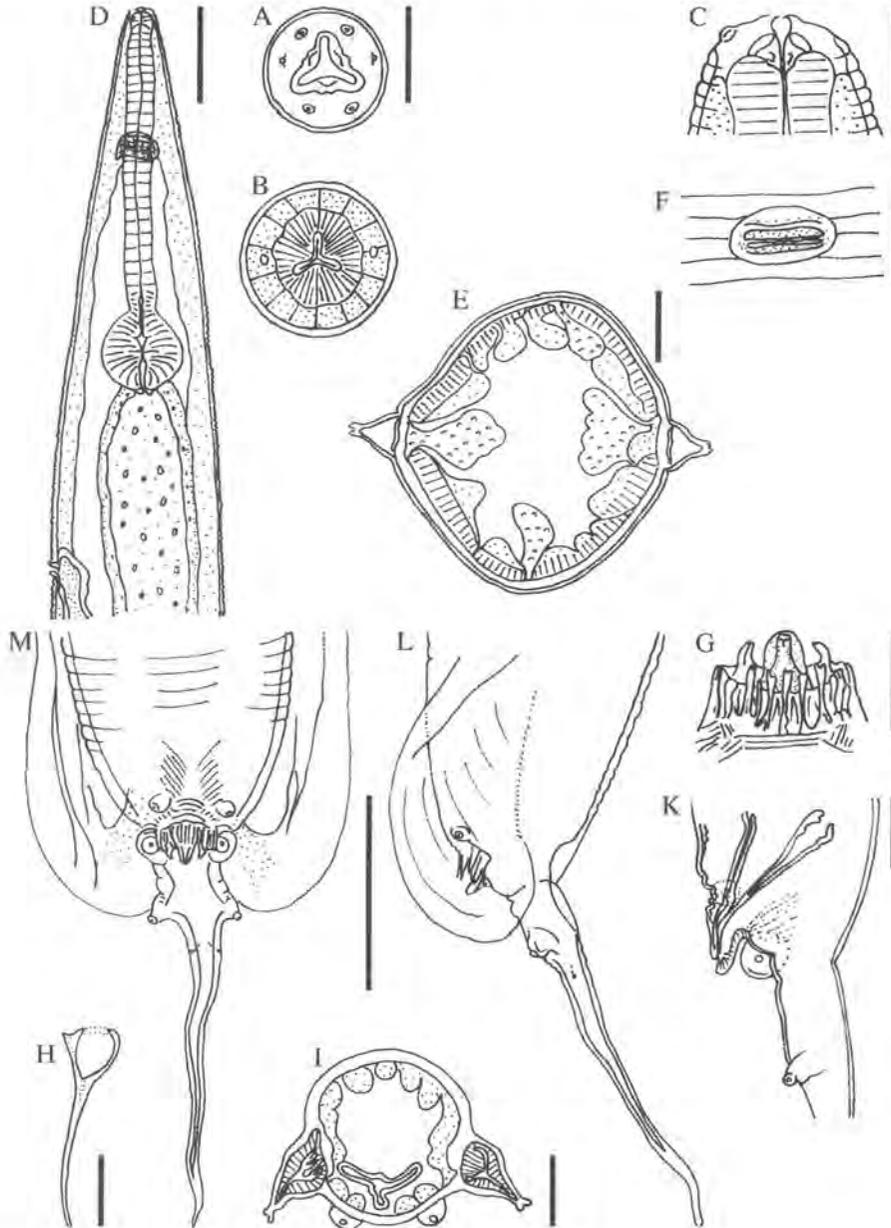


FIG. 12 *Skrjabinodon mabuyae* male from *Mabuya striata*

- 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

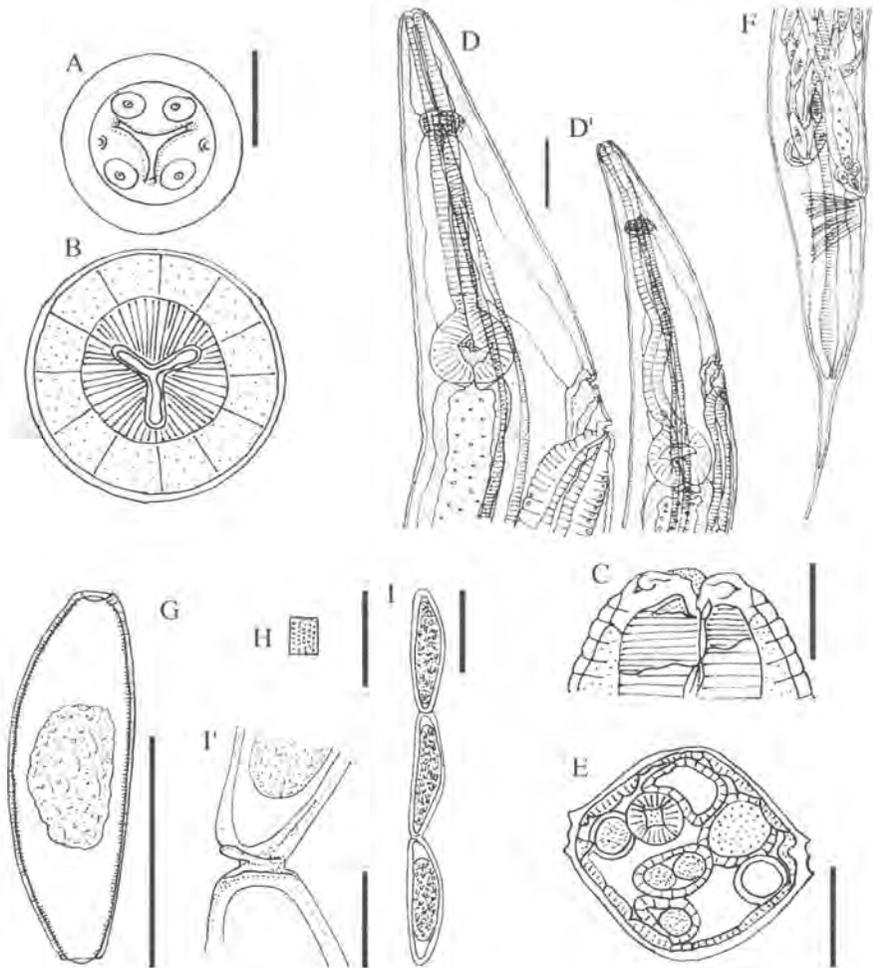


FIG. 13 *Skrjabinodon mabuyae* female from *Mabuya striata*

- 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 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.

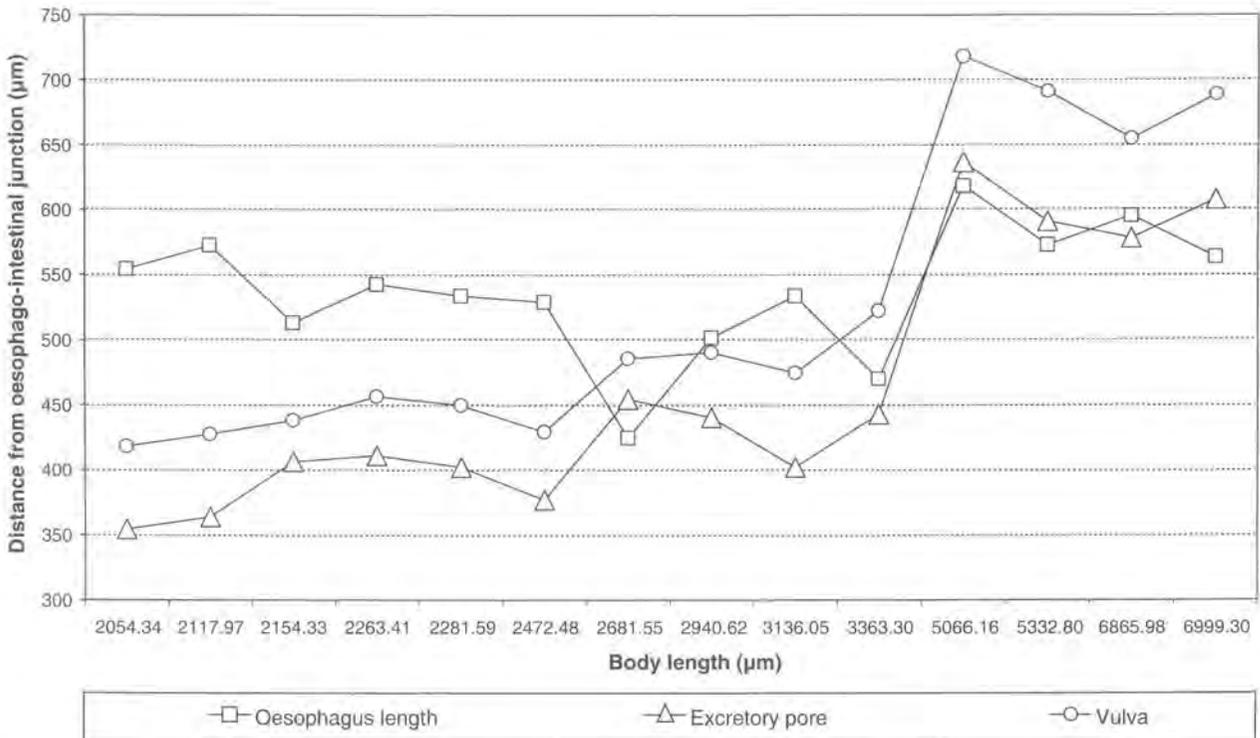


FIG. 14 The relationship between the body length, length of the oesophagus, and the position of the vulva and excretory pore in adult and subadult *Skrijabinodon mabuyae* females

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) \times 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 synonymy but it was not possible to trace the type specimens and the present specimens are therefore assigned to *S. mabuyae*.

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