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.

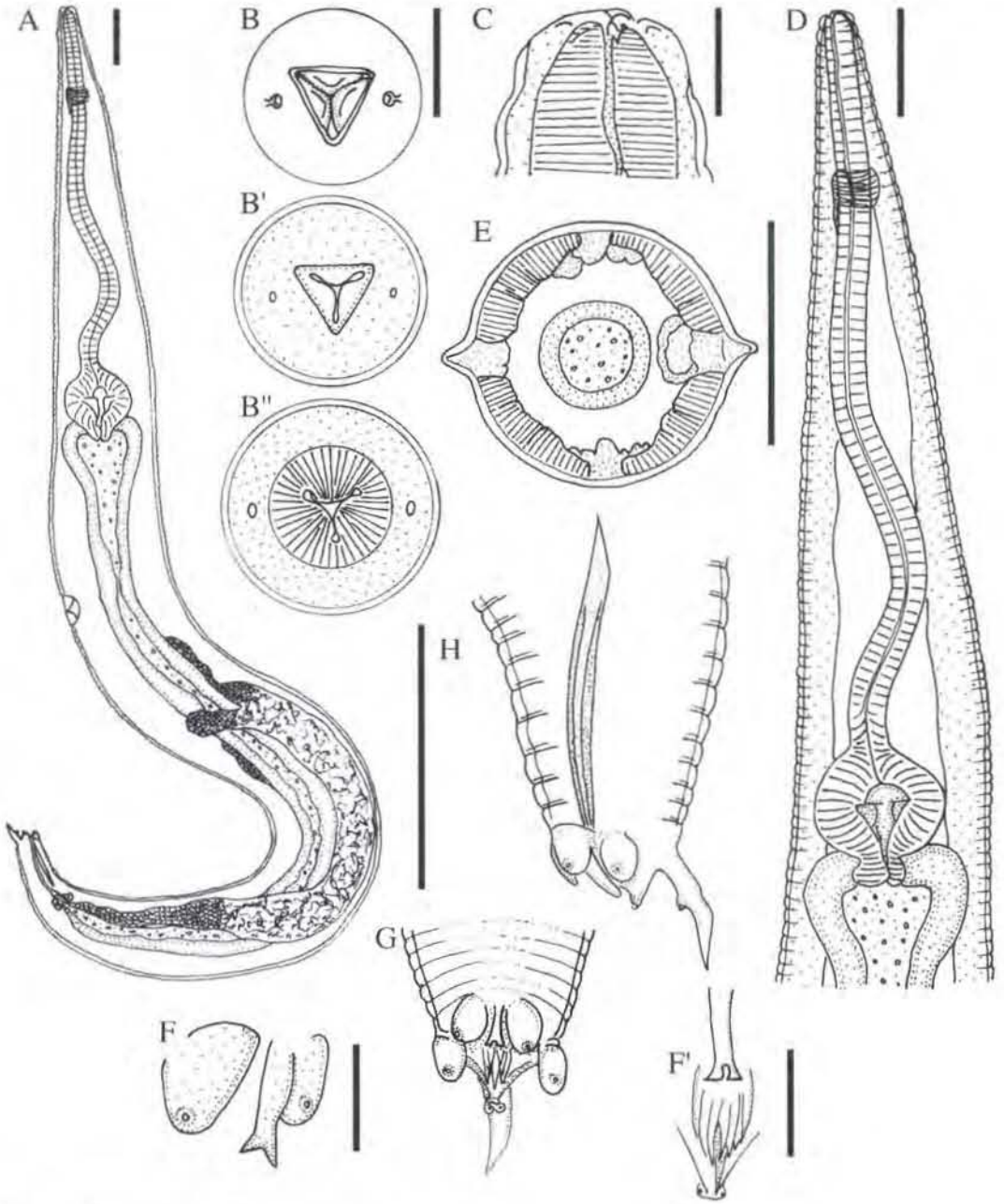

FIG. 1 *Thelandros schusteri*, male

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

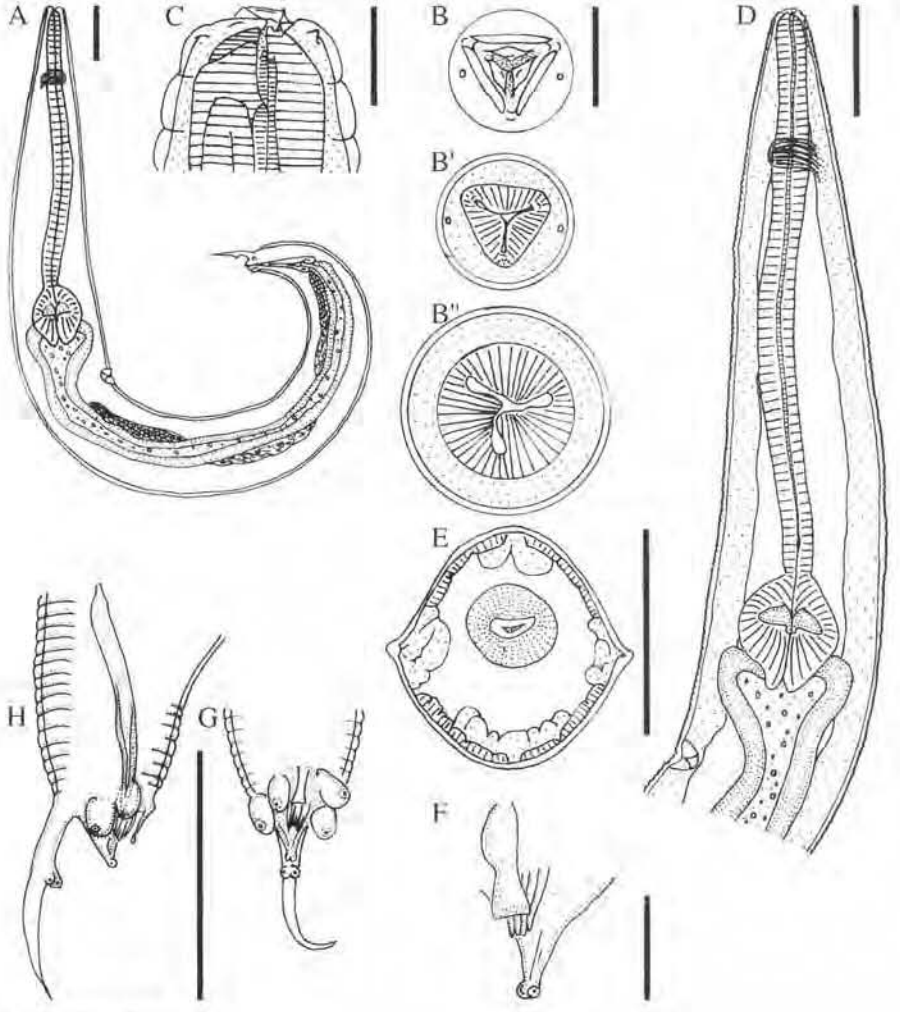

FIG. 2 *Thelandros boomkeri*, male

- 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).

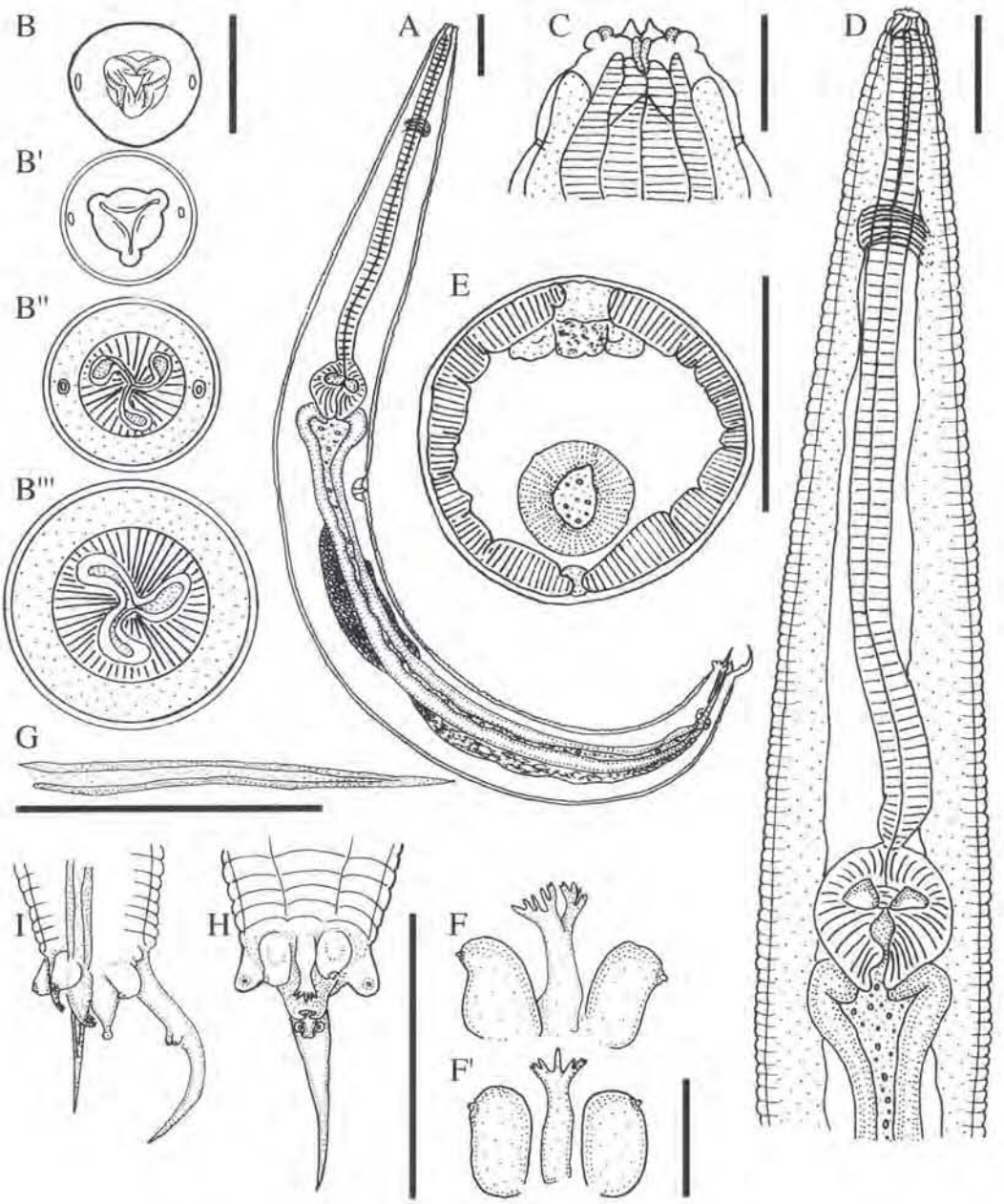

FIG. 3 *Thelandros luciusi*, male

- 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

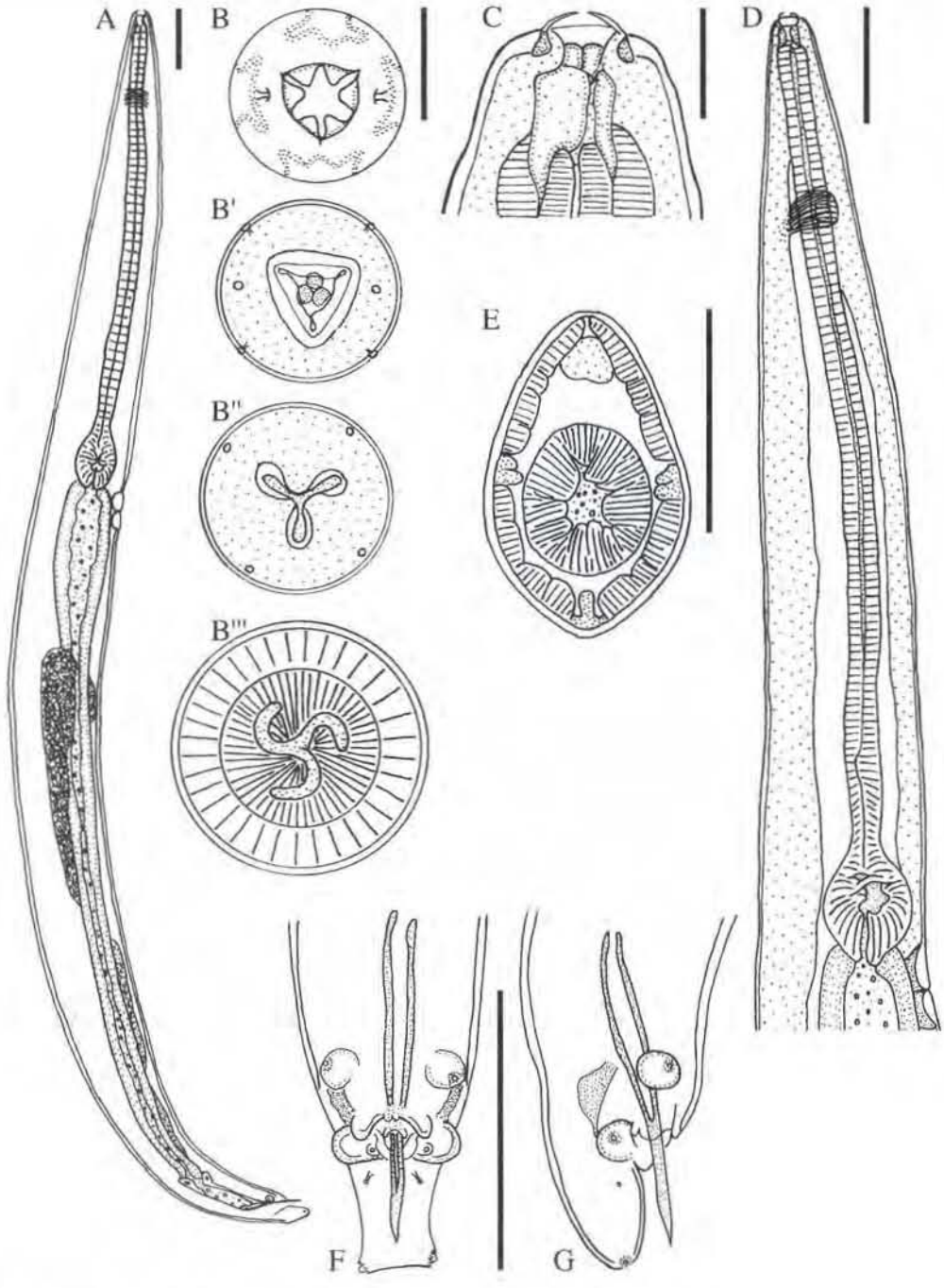

FIG. 4 *Tachygonetria bainae*, male

- 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

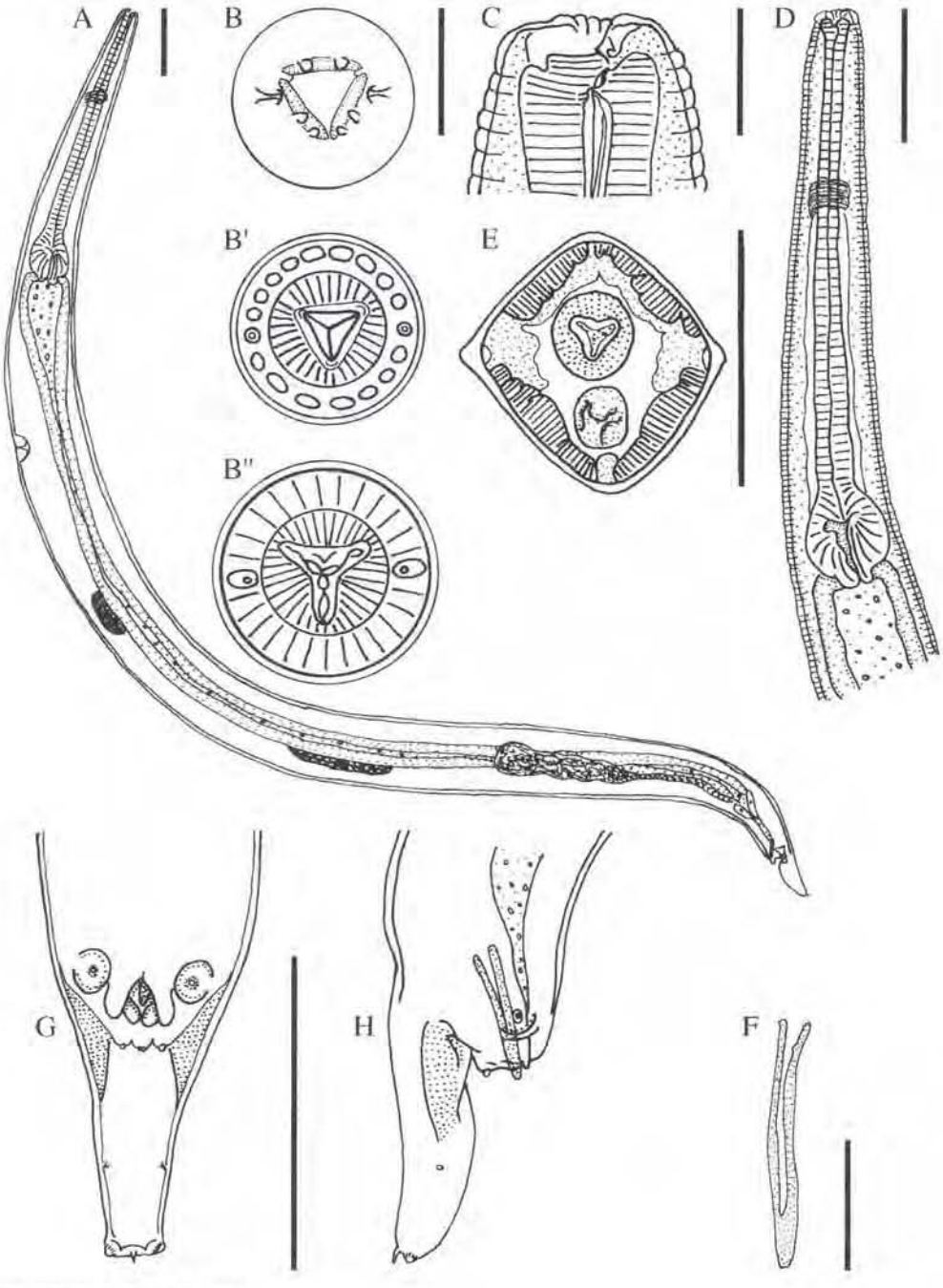

FIG. 5 *Tachygonetria petterae*, male

- 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-*

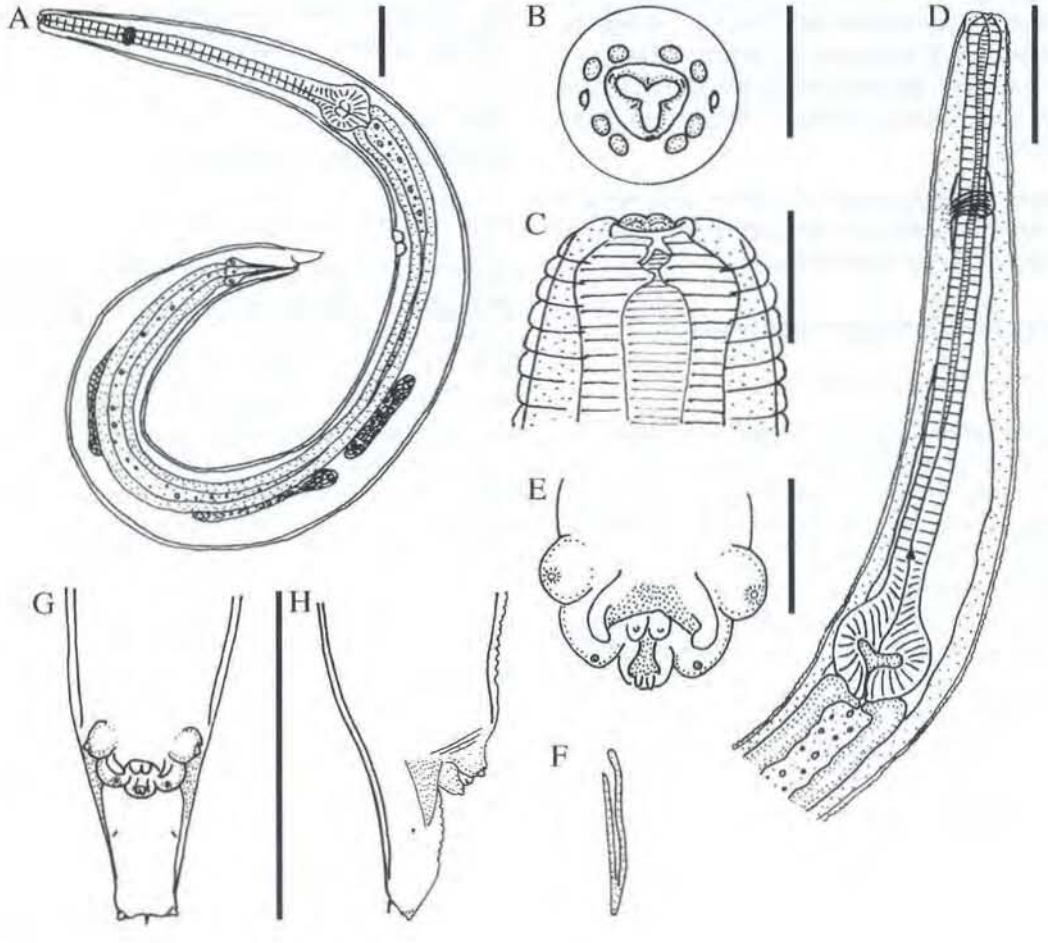

FIG. 6 *Tachygonetria chabaudi*, male

- 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.

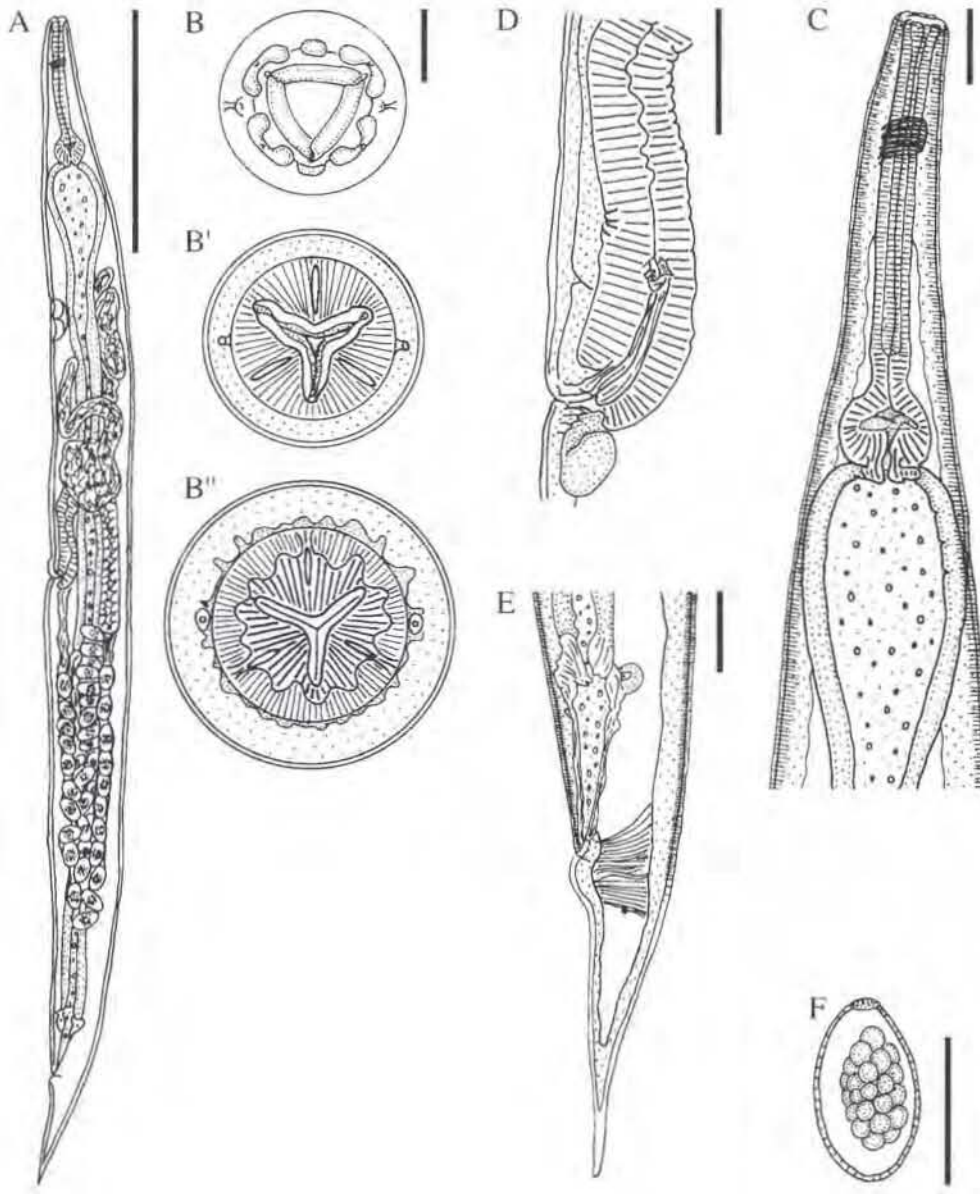

FIG. 7 Female type A

- 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-

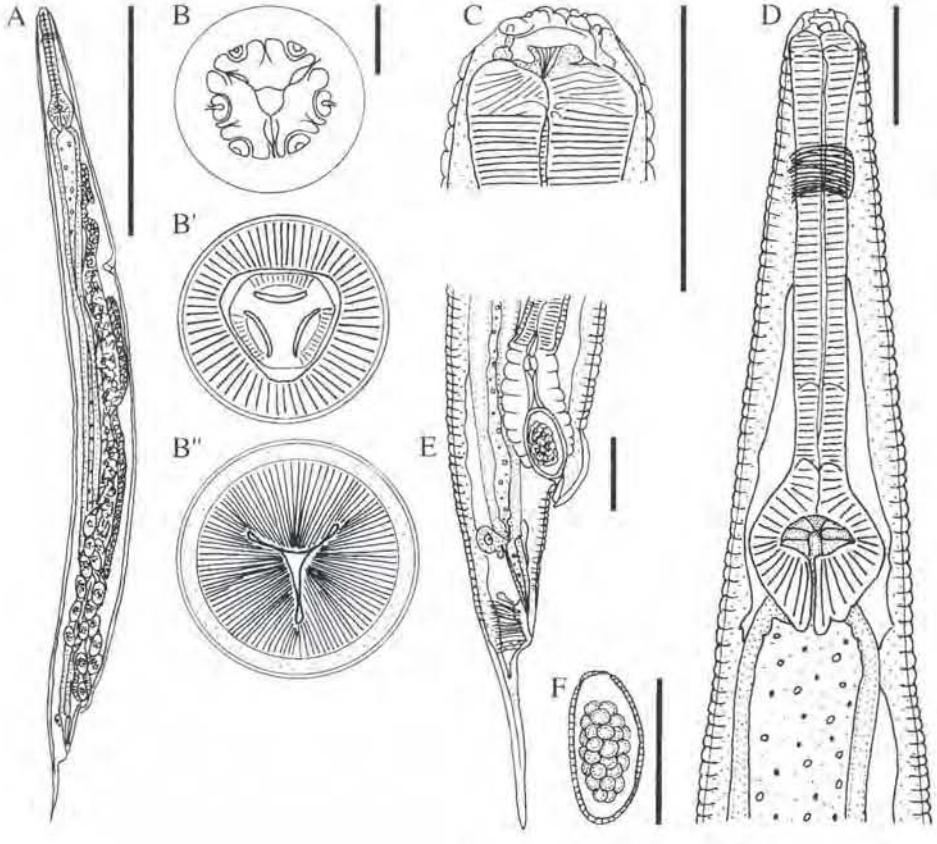

FIG. 8 Female type B

- 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

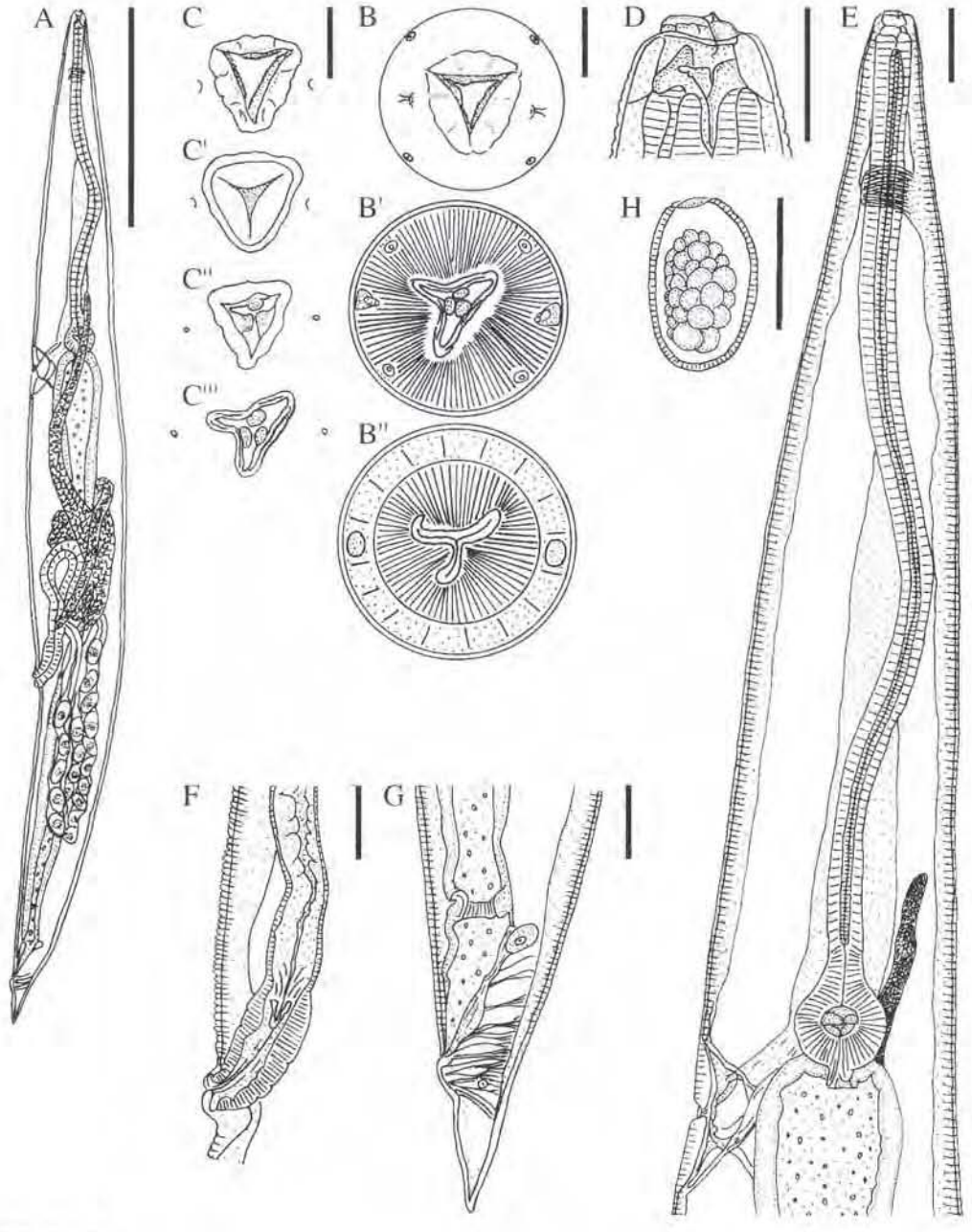

FIG. 9 Female type C

- 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

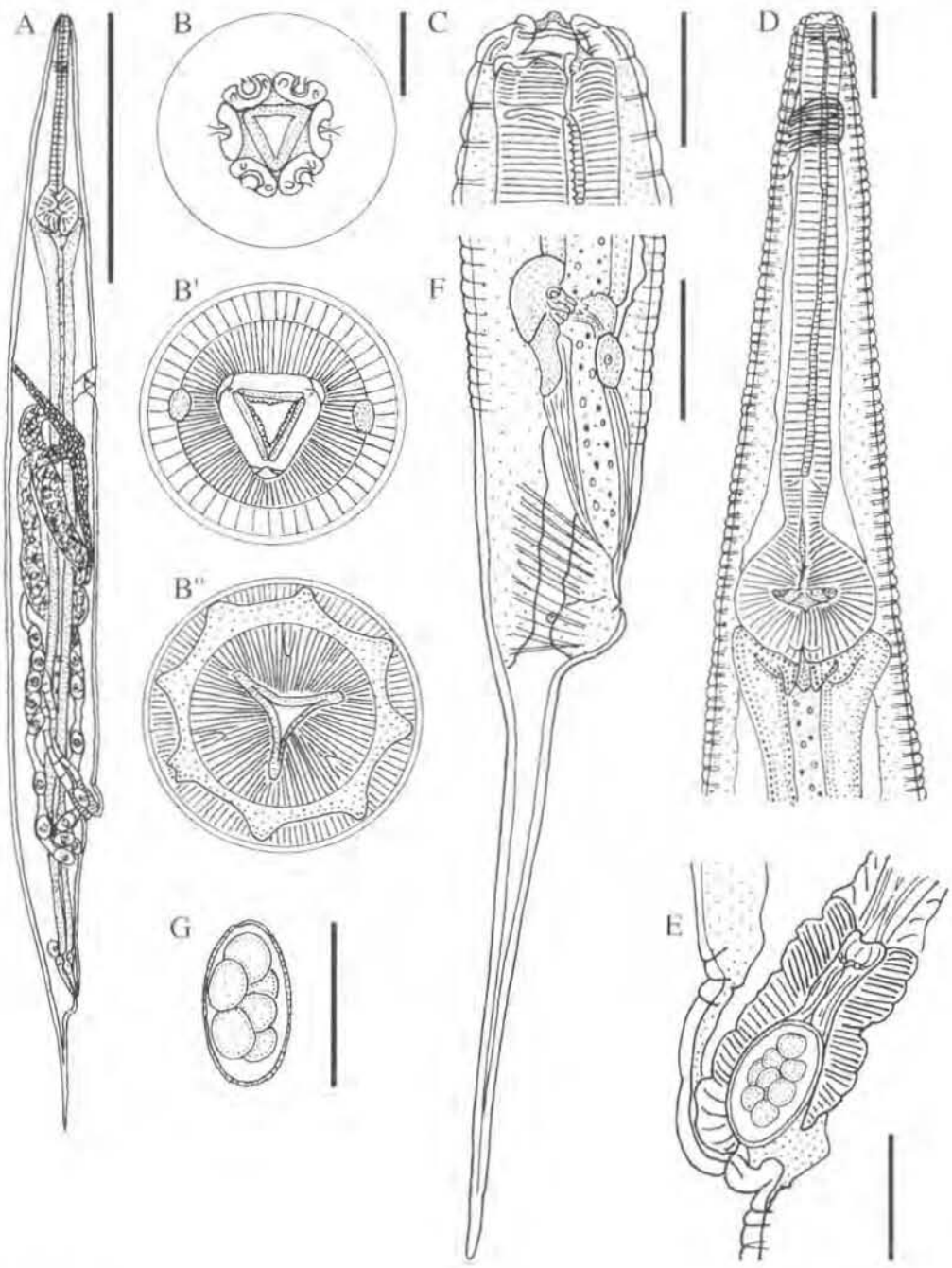

FIG. 10 Female type D

- 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

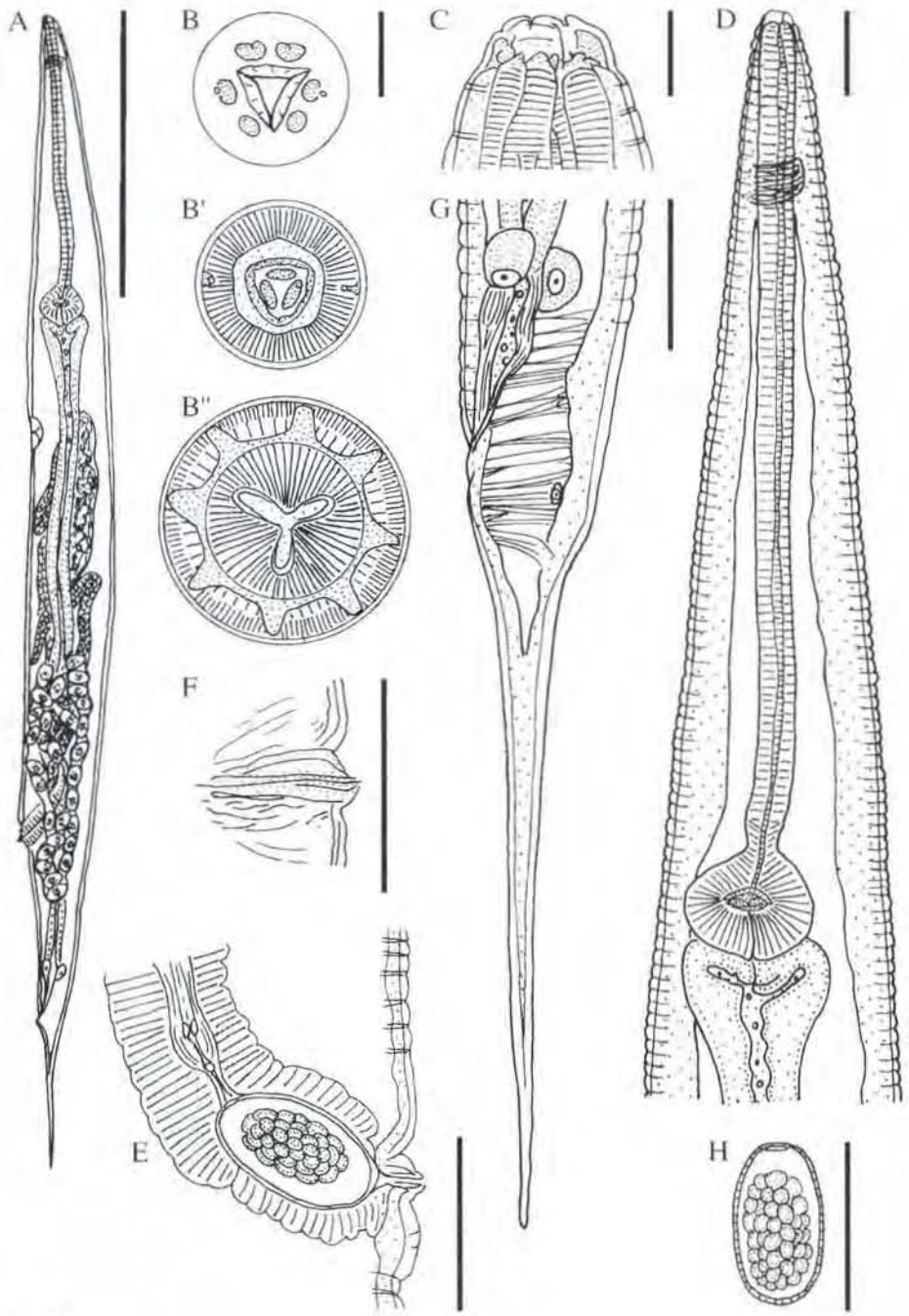

FIG. 11 Female type E

- 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

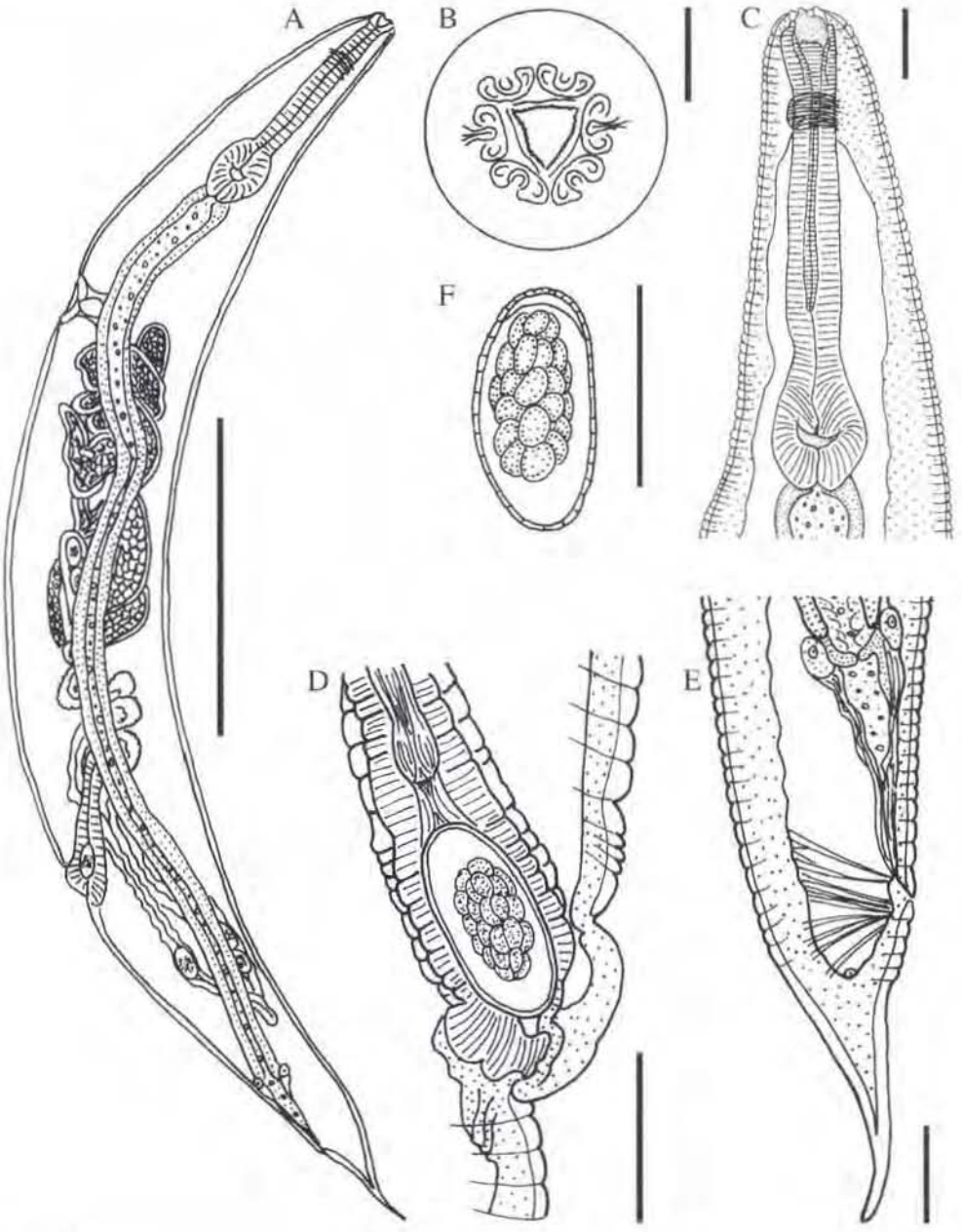

FIG. 12 Female type F

- 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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