

Observations on the life-cycles and larval morphogenesis of *Haemonchus bedfordi*, *Impalala tuberculata* and *Longistrongylus sabie* (Nematoda: Trichostrongyloidea) parasitic in impala, *Aepyceros melampus*

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The previously unknown life-cycles of *Haemonchus bedfordi*, *Impalala tuberculata* and *Longistrongylus sabie* parasitic in impala, are recorded. Observations on the morphology of the developmental stages and their habitat of these three nematode species are described. The similarities and differences to closely related species or subspecies are discussed. The morphology of the developmental stages of *Haemonchus bedfordi* are compared to the *Haemonchus* spp., *H. contortus* and *H. placei*.

Die voorheen onbekende lewensiklusse van *Haemonchus bedfordi*, *Impalala tuberculata* and *Longistrongylus sabie*, wat parasities voorkom in rooibokke, word beskryf. Morfologiese ondersoeke van die ontwikkelingsstadia van hierdie drie nematode-spesies word beskryf en hul habitat, ooreenkomste en verskille, met naverwante spesies en subspecies, word bespreek. Die morfologie van die ontwikkelingsstadia van *Haemonchus bedfordi* word vergelyk met *Haemonchus* spp., *H. contortus* en *H. placei*.

A two-year study (March 1973–75) on helminths of impala, *Aepyceros melampus* (Lichtenstein, 1912) in Natal (Anderson 1980), presented the opportunity to observe the hitherto unknown aspects of larval morphogenesis, in this way completing the gap in the life-cycles of certain parasitic nematodes of this species of antelope. Previous reports which emanated from the two-year study include the life cycle of *Pneumostrongylus calcaratus* Mönnig, 1932, (Heinichen 1974; Heinichen Anderson 1976, Anderson 1982), *Cooperia fuelleborni* (Anderson 1986) and *Cooperioides hamiltoni* and *C. hepatica* (Anderson 1992). These helminth collections also made it possible to study the life-cycles of *Haemonchus bedfordi* Le Roux, 1929, *Impalala tuberculata* Mönnig, 1923 and *Longistrongylus sabie* Mönnig, 1932.

The developmental stages of *H. bedfordi* were compared to those of *H. contortus* and *H. placei*.

Materials and Methods

The studies were carried out on the Nyala Game Ranch of Mr Scott-Barnes, situated 20 km north-west of Empangeni in Natal. Two impala were examined each month for a period of two years. To recover all the worms from the intestine the contents were put into a modified Baermann apparatus and placed into Shone's waterbath. More details of this method were published previously (Heinichen 1973). Adult, fifth-stage and fourth-stage larvae (L4) *H. bedfordi*, *L. tuberculata* and *L. sabie* were recovered from the ingesta of the small intestine.

Table 1 Comparison of dimensions (μm) of infective larvae of *Haemonchus* species

Species	<i>Haemonchus bedfordi</i>		<i>Haemonchus contortus</i>						<i>Haemonchus placei</i>			
	Impala		Sheep						Cattle			
Author	These results		Veglia (1915)		Dikmans & Andrews (1933)		Mönnig (1931)		Keith (1953)		Soulsby (1965)	
Dimensions	Range	Mean \pm S.D.	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Total length	615–718	644,3 \pm 37,1	–	715	650–751	693	694–772	733	750–850	–	682–780	739
Length of oesophagus	108–139	125,6 \pm 11,1	–	175	122–150	141	127–145	141	–	–	135–164	149
Distance from excretory pore to anterior end	87–98	93,0 \pm 4,5	–	80	–	–	–	–	–	–	–	–
Distance from nerve ring to anterior end	78–91	84,4 \pm 4,9	75,80	–	–	–	–	–	–	–	–	–
Genital primordium:												
Length	9–16	11,4 ^a	–	9,5	–	–	–	–	–	–	–	–
Width	5–13	7,2 ^a	–	8,0	–	–	–	–	–	–	–	–
Distance from genital primordium to tail	273–358	309,8 ^a	–	325	340–366	348	341–392	373	–	–	362–380	394
Distance from anus to tip of tail sheath	103–137	119,9 \pm 15,8	–	130	119–146	134	145–165	149	160–190	–	97–142	118
Distance from tail to sheath	62–86	76,0 \pm 9,7	–	70	65–78	73	82–94	82	90–110	–	55–82	66

^a Only five worms measured

Recovery of the third-stage larvae (L3) of these parasites followed the method for *Cooperia fuelleborni* larvae (Anderson 1986). For the recovery of the first-stage larvae (L1) and the second-stage larvae (L2) of *H. bedfordi* and *L. sabie* the culture method of Whitlock (1956), modified by Reinecke (1961) was used. A small sample of the faeces from the culture was removed by forceps after two to three days and examined under the microscope for L1. This procedure was repeated after seven to eight days to recover the L2. The larvae were removed, placed on a glass slide, heat-killed and examined in a drop of water. The morphological measurements and drawings of all helminths were carried out as published previously for *C. fuelleborni* (Anderson 1986).

Results

Preparasitic stages

H. bedfordi

The width of the L3 varied from 8–12 μm ($9,6 \pm 1,8$; mean \pm S.D.) at the anterior end, from 20–23 μm ($21,4 \pm 1,0$) across the oesophagus and from 9–16 μm ($12,7 \pm 3,0$) across the anus. The maximum width varied from 20–23 μm ($21,4 \pm 1,00$). The oesophagus was 7–9 μm ($8,3 \pm 0,8$) wide.

In Table 1 the measurements of the L3 are compared with those of other *Haemonchus* species occurring in cattle and sheep. Figure 1a shows the features of the infective larvac. As is typical for the genus *Haemonchus*, this L3 also has a long, whip-like sheath on the posterior end and its intestine is composed of 16 cells (Figure 1a).

L. sabie

The features of the L3 of *L. sabie* are shown in Figure 1(b). The intestine was composed of 16 cells.

The total length of the L3 varied from 632–718 μm ($667,8 \pm 34,2$). The width of the L3 varied from 6–8 μm ($7,7 \pm 0,8$) at the anterior end, from 14–29 μm ($21,5 \pm 4,8$) across the oesophagus and from 13–17 μm ($14,3 \pm 1,4$) across the anus. The maximum width varied from 14–29 μm ($21,5 \pm 4,8$). The oesophagus was 4–13 μm ($8,3 \pm 3,0$) wide and 138–156 μm ($145,7 \pm 7,2$) long. The distance of the excretory pore and the nerve ring from the anterior end varied from 91–108 μm ($102,5 \pm 6,4$) and 85–103 μm ($96,0 \pm 6,4$) respectively. The length of the genital primordium varied from 7–12 μm (9,6 mean) and its width from 5–8 μm (6,8). In five worms the genital primordia were situated 293–347 μm (321,2) from the posterior end. The distance from the anus to the tip of the tail sheath varied from 87–135 μm ($104,7 \pm 17,0$) and the distance from the larval tail to the sheath from 34–81 μm ($49,5 \pm 17,1$).

Parasitic stages

H. bedfordi

The measurements of male and female L4 and 5th-stage *H. bedfordi* are summarized in Table 2 and their features shown in Figure 2 and 3. Some of these measurements are compared with those of other species of this genus in Table 3. The genital primordium seen in the L3, was replaced by developing testes in the L4. Figure 2e shows a male in the fourth moult; spicules are present, but not well sclerotized and the bursa has started to develop. In the late L4 female the vulvar region has



Figure 1 Infective larvae of: (a) *Haemonchus bedfordi*; (b) *Longistrongylus sabie*.

started to develop, but no vulvar flap is present as yet (Figure 2d). In the 5th stage the cervical papillae are well developed and the vulvar flap is present (Figure 3a and d). There are 32–35 longitudinal, cuticular ridges observed in the midbody region (Figure 3c).

I. tuberculata

The measurements of male and female L4 and 5th-stage *I. tuberculata* are listed in Table 4 and their features are shown in Figures 4 and 5. In the early L4, males and females cannot be differentiated from one another (Figure 4b).

Larvae of *I. tuberculata*, however, are easily distinguished from other larvae present in the intestine because the whole worm is tightly coiled, there are two very small round structures in the anterior part of the buccal cavity and the tail has three subterminal papillae.

In the late L4 the male (Figure 4c) can easily be distin-

Table 2 Dimensions of parasitic stages of *Haemonchus bedfordi*

Stages of development	Male				Female					
	L4		5th		Early L4		Late L4		5th	
Dimensions ^a	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Total length (mm)	1,3–4,1	3,3±1,1	4,4–9,2	6,0–1,5	1,4–3,8	2,2±0,9	4,0–6,4	4,8±0,7	7,6–12,1	10,4±1,6
Width: At anterior end	13–27	2,0±4,8	24–30	26,4±1,9	12–22	15,1±3,5	19–30	24,1±3,7	27–43	33,1±4,6
Across oesophagus	27–84	65,1±19,0	81–149	99,6±23,0	25–68	38,4±15,6	59–146	87,3±23,3	108–176	152,1±20,5
Maximum	23–95	71,5±25,4	78–216	121,2±39,5	16–30	26,7±9,4	76–135	91,3±18,1	135–243	207,3±30,1
At vulva	–	–	–	–	–	–	76–135	91,3±18,1	135–243	184,7±34,1
In front of bursa	23–95	71,5±25,4	78–216	121,2±39,5	–	–	–	–	–	–
At anus	–	–	–	–	18–39	24,0±6,5	38–59	43,8±6,4	54–92	76,2±11,5
Oesophagus: Length	292–594	497,7±110,1	621–994	816,0±117,7	274–486	342,7±87,3	520–945	628,3±124,0	886–1231	1109,1±129,6
Width at base	20–51	40,5±11,0	46–97	64,7±15,5	16–30	26,7±9,4	35–95	52,6±17,3	59–103	86,0±14,9
Distance from cephalic papillae to anterior end	–	–	281–351	323,9±29,7	–	–	254–367	309,2±45,2	335–421	376,3±28,3
Distance from excretory pore to anterior end	136–260	210,5±38,3	230–308	265,3±29,3	130–235	178,5±33,6	230–302	256,2±25,5	274–351	314,4±26,3
Distance from nerve ring to anterior end	127–230	187,3±30,7	189–277	233,2±28,5	113–211	155,5±30,7	189–286	227,8±30,2	244–292	276,5±17,0
Genital primordium: Length	–	–	–	–	91–260	139,3±45,3	–	–	–	–
Width	–	–	–	–	7–14	10,8±2,5	–	–	–	–
Distance from genital primordium to tail	–	–	–	–	202–702	366,0±164,2	–	–	–	–
Length of ovijectors	–	–	–	–	–	–	287–621	511,0±102,3	518–729	616,1±62,5
Distance from vulvar opening to tail (mm)	–	–	–	–	–	–	0,7–1,4	0,9±0,2	1,3–2,2	1,8±0,3
Distance from anus to tail	–	–	–	–	65–178	94,9±35,3	135–216	150,3±23,9	194–302	258,5±38,8
Length of spicules	–	–	260–394	344,6±50,3	–	–	–	–	–	–
Gubernaculum	–	–	78–189	121,7 ^b	–	–	–	–	–	–

^aAll measurements are given in μm unless stated otherwise. ^bOnly three worms measured

guished from other larvae present in the intestine because the whole worm is tightly coiled, there are two very small round structures in the anterior part of the buccal cavity and the tail has three subterminal papillae.

In the late L4 the male (Figure 4c) can easily be distinguished from the female by its swollen posterior end. In some males the genital primordium had divided into only a few cells, while others showed developing testes. Figure 4e shows a male in the fourth moult. Two of the three papillae are still visible and the spicules and bursa have started to develop. Contrary to most of the other species studied, the vulvar region of the L4 female in *I. tuberculata* is rather under developed. The ovijector is not yet visible (Figure 4d). In the 5th stage, however, the vulvar region has developed and the ovijector is visible (Figure 5b). There are 10 large, longitudinal, cuticular ridges observed in the midbody region (Figure 5d).

The spicule length of *I. tuberculata* in two 18-month-old and in two adult impala was compared by measuring 10 specimens from each animal. In the impala aged 18 months

the spicule length of *I. tuberculata* varied from 574–736 μm ($666,6 \pm 48,1$) and 601–744 μm ($674,8 \pm 43,4$) and in the adults from 652–736 μm ($681,0 \pm 30,2$) and 662–780 μm ($709,8 \pm 43,5$).

L. sabie

The measurements of male and female L4 and the 5th-stage *L. sabie* are given in Table 5 and their features illustrated in Figure 6 and 7. Two small, rod-like structures are visible in the buccal cavity of L4 (Figure 6a). These structures are similar to those described by Douvres (1956) in *Ostertagia*. In the 5th stage the vulvar region has developed and the ovijectors are visible (Figure 7b). There are 25 longitudinal, cuticular ridges observed in the midbody region (Figure 7c).

Habitat of parasitic larval stages

H. bedfordi

The life-cycle of *H. bedfordi* was found to be similar to that of *H. contortus* as described by Veglia (1915).

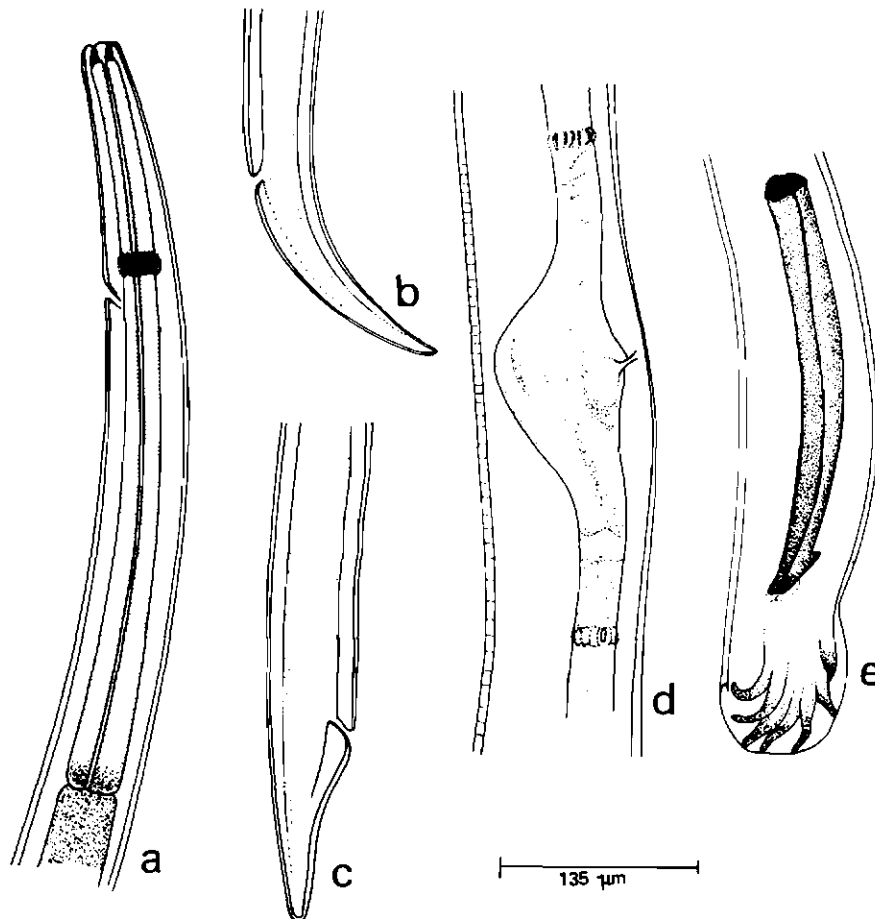


Figure 2 L4 of *Haemonchus bedfordi*: (a) Anterior end of female, (b) Posterior end of female, (c) Posterior end of male, (d) Vulvar region of late L4 female, (e) Posterior end of male in moulting.

Table 3 Comparison of dimensions of parasitic larval stages of three species of *Haemonchus*^a

Species	Host	Author	Days after infestation	Stage	Sex	Total length (mm)	Distance from cervical papillae		Oesophagus length	Oesophagus width	Distance from genital primordium to tail	Length of genital primordium	Distance from vulva opening to tail (mm)	Distance from anus to tail	Length of spicules
							to ant. end	Maximum width							
<i>Haemonchus placei</i>	Cattle	Bremner (1956)	2-3	L4	-	0,6-0,9	-	-	-	-	-	-	-	-	-
<i>Haemonchus contortus</i>	Sheep	Veglia (1915)	Just after ecdysis	L4	-	0,8-1,0	-	22-25	160-200	20-23	250-300	18-25	-	-	-
				L4	M	2,7-4,1	-	55-85	-	-	-	50-70	-		
			L4	F	3,7-5,0	-	70-95	-	-	-	132	-			
<i>Haemonchus bedfordi</i>	Impala	These results	-	L4	M	1,3-4,1	-	-	23-95	292-594	20-51	-	-	-	-
				Early L4	F	1,4-3,8	-	16-30	274-486	16-30	202-702	91-260	-	65-178	-
				Late L4	F	4,0-6,4	-	76-135	520-945	35-95	-	-	-	-	-
<i>Haemonchus contortus</i>	Sheep	Veglia (1915)	11-14	5th stage	M	5-8	714	90-130	750	96	-	-	-	-	320-356
					F	6,5-10,0	-	90-150	-	-	-	-	1,5	-	-
<i>Haemonchus bedfordi</i>	Impala	These results	-	5th stage	M	4,4-9,2	281-351	78-216	621-994	46-97	-	-	-	-	260-394
					F	7,6-12,1	335-421	135-243	886-1231	59-103	-	-	1,3-2,2	-	-

^a All measurements are given in µm unless stated otherwise



Figure 3 Fifth stage of *Haemonchus bedfordi*: (a) Anterior end of female, (b) Posterior end of female, (c) Posterior end of male, (d) Vulvar region of female, (e) Cross section of male in the midbody region.

L. tuberculata

As in the case of *Cooperia* species the L3 of *I. tuberculata* probably do not migrate deeply into the mucosa. Numerous L4 were present in the ingesta of the proximal part of the small intestine. The 5th stage was found throughout the small intestine, while the adult worms were also numerous in the distal part of the small intestine.

L. sabie

Many L4, but only a few 5th-stage worms were found in the

scrapings of the abomasal mucosa. On the other hand few L4, but more 5th-stage worms were found in the abomasal contents.

Discussion

Wetzel & Fortmeyer (1960) fully described the L3 of *I. tuberculata* var. *longispiculata*, which is regarded as a synonym of *I. tuberculata* by Boomker (1977) in his revision of the genus *Impalaia*.

Very little research, however, has been carried out on the L3 of *H. bedfordi* and *L. sabie* and the L4 and 5th stage of all

Table 4 Dimensions of the parasitic stages of *Impalaila tuberculata*

Sex	Male&female		Male				Female			
	Early L4		Later L4		5th		Late L4		5th	
Stages of development	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Dimensions ^a										
Total length (mm)	1,3–1,8	1,5±0,2	2,3–3,8	3,0±0,5	4,4–7,4	5,8±1,0	3,0–6,2	4,6±1,1	9,4–14,2	12,2±2,0
Width: At anterior end	16–19	16,9±1,1	16–24	20,5±3,0	26–38	29,5±3,7	21–27	25,2±2,4	30–41	36,0±4,3
Across oesophagus	26–34	30,8±2,9	35–57	46,2±6,6	43–81	55,6±11,7	39–78	57,1±11,0	54–86	66,6±12,1
Maximum	34–44	37,0±4,0	43–78	57,4±12,7 ^c	65–130	90,6±19,3 ^c	30–86	61,3±17,8	81–135	108,7±22,0
At vulva	–	–	–	–	–	–	30–86	55,6±15,4	61–108	85,9±16,2
In front of bursa	–	–	–	–	65–130	90,6±19,3	–	–	–	–
At anus	16–23	17,9±2,7	36–70	53,0±12,1	–	–	19–24	21,5±1,8	–	–
Oesophagus: Length	234–264	248,3±9,9	260–416	313,3±44,5	313–425	371,6±39,5	274–578	355,1±88,0	395–486	446,2±32,6
Width at the base	16–20	18,3±1,9	21–35	26,5±3,9	23–38	28,3±4,7	25–43	30,5±5,8	22–46	36,2±7,5
Distance from excretory pore to anterior end	192–221	202,6±9,4	216–260	231,9±14,6	233–341	288,6±29,3	208–286	256,8±22,0	264–422	314,0±43,7
Distance from nerve ring to anterior end	159–188	171,2±9,4	183–233	211,4±14,6	200–333	266,1±35,5	190–248	226,3±22,9	241–381	282,2±40,6
Genital primordium:										
Length	6–22	9,1 ^b	testes began to develop	–	–	–	–	–	–	–
Width	4–8	5,3	testes began to develop	–	–	–	–	–	–	–
Distance from genital primordium to tail	78–120	100,6 ^b	testes began to develop	–	–	–	–	–	–	–
Length of ovjectors	–	–	–	–	–	–	149–238	183,0 ^b	297–497	381,8±84,8
Distance from vulvar opening to tail (mm)	–	–	–	–	–	–	111–176	149,4±21,7	162–205	180,4±18,1
Distance from anus to tail	35–42	38,0±2,2	38–76	51,2±11,1	–	–	39–55	47,6±6,4	33–62	46,4±8,9
Length of spicules	–	–	–	–	601–799	662,2±64,3	–	–	–	–
Gubernaculum	–	–	–	–	43–78	59,9±10,8	–	–	–	–

^a All measurements are given in μm unless stated otherwise. ^b Only seven worms measured. ^c In the male L4 and 5th stage the maximum width measured across the swelling of the tail.

three of these parasites. From Table 1 it is evident that the L3 of *H. bedfordi* are slightly shorter than those of *H. contortus* and *H. placei*. The larval tail and sheath of *H. bedfordi* are slightly shorter than that of *H. contortus*, but approximately the same length as in *H. placei*. The sheath of *H. bedfordi* extending beyond the larval tail is similar to the whip-like filament found in *H. contortus* and *H. placei*.

The L3 of *L. sabie* (Figure 1b) can only be distinguished from the L3 of *Cooperia fuelleborni* (Anderson 1986) and the *Cooperioides* species (Anderson 1992) by the presence of a slight 'kink' in the tail and sheath at the posterior end of the larval tail, which is also slightly swollen. This latter distinguishing characteristic becomes more pronounced in the adult (Mönnig 1933). These larvae do not have the whip-like sheath characteristic of *H. bedfordi* (Figure 1a).

Table 3 shows that the measurements of the L4 and 5th-stage *H. bedfordi* are similar to those of *H. contortus* as recorded by Veglia (1915) except that in the 5th stage the cervical papillae of *H. bedfordi* are much closer to the anterior end than in *H. contortus*. Mönnig (1931) found that the tail sheath of *H. bedfordi* was longer than that of *H. contortus* but this was not confirmed in this investigation. The cervical papillae were not observed in the early L4, but were present in the late L4. In *H. placei*, however, Bremner (1956) observed cervical papillae five days after infestation, that is,

in the early L4. Veglia (1915) referred to the presence of cervical papillae only in the adult *H. contortus*.

Contrary to the observations of Mönnig (1924) no hooks were observed on the proximal end of the spicules in the 5th stage or adult worms. In the latter, a median process was observed at the proximal end of the spicule similar to those described by Boomker (1977).

Mönnig (1924) recorded the spicule length of *I. tuberculata* from the Transvaal as 600 μm , but more recently Boomker (1977) in his revision of the genus *Impalaila*, re-examined Mönnig's type specimens (Onderstepoort Helminthological Collection No. T 2010) and found the spicule length to vary from 850–858 μm . In other material from impala, Boomker found the spicule length to vary from 804–851 μm and suggested that the variation in spicule length may be due to the immune status of the host. This is in agreement with the findings of Keith (1967) who found that spicules of *Cooperia pectinata* were shorter in animals which had previously been exposed to the nematode. According to Keith (1967) the reduction in spicule length was due to a host reaction, stimulated by prior infestation and cannot be attributed directly to the presence of survivors of a previous infestation.

No significant difference was found in the spicule length of *I. tuberculata* in young or old impala and therefore these measurements agree more closely with those of Mönnig

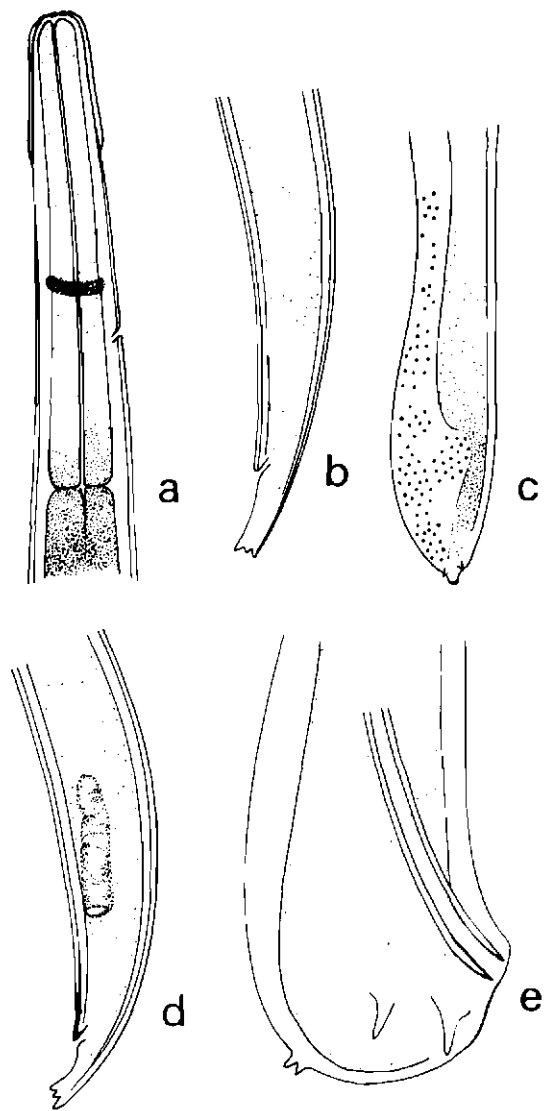


Figure 4 L4 of *Impalaia tuberculata*: (a) Anterior end of female, (b) Posterior end of early L4 (male & female), (c) Posterior end of male (late L4), (d) Posterior end of female (late L4), (e) 4th moult in male.

(1924) than with those of Boomker (1977).

Contrary to the observation of Ortlepp (1963) on *Bigalke-
nema namaquensis* Ortlepp, 1963 and Gibbons (1972) on
Kobusinema banagiense Gibbons, 1972, there is no differenti-
ation of the oesophagus into an anterior muscular region and
a posterior non-muscular region in *L. sabie*. Gibbons (1977)
synonymized *Bigalkenema* and *Kobusinema* with the earlier
genus *Longistrongylus* and transferred all species of these two
genera to *Longistrongylus*. The valid name of *Bigalkenema
sabie* thus becomes *Longistrongylus sabie*.

Horak (1978) stated that the morphology of the adult *L.
sabie* is similar to that of the *Ostertagia* species. He also
found that he could use the description of Douvres (1956) for
the L4 of *Ostertagia ostertagi* to identify L4 of *L. sabie*.
During the present studies it was also found that the L4 of *L.
sabie* is very similar to that of *Ostertagia ostertagi* in that it
has two rod-like structures at the anterior end like those previ-
ously described by Douvres (1956) in *Ostertagia ostertagi*.
Cephalic papillae are also present in the 5th stage. Therefore,
from studies of both larvae and adult, it is clear that *L. sabie*
is very closely related to the *Ostertagia* species.

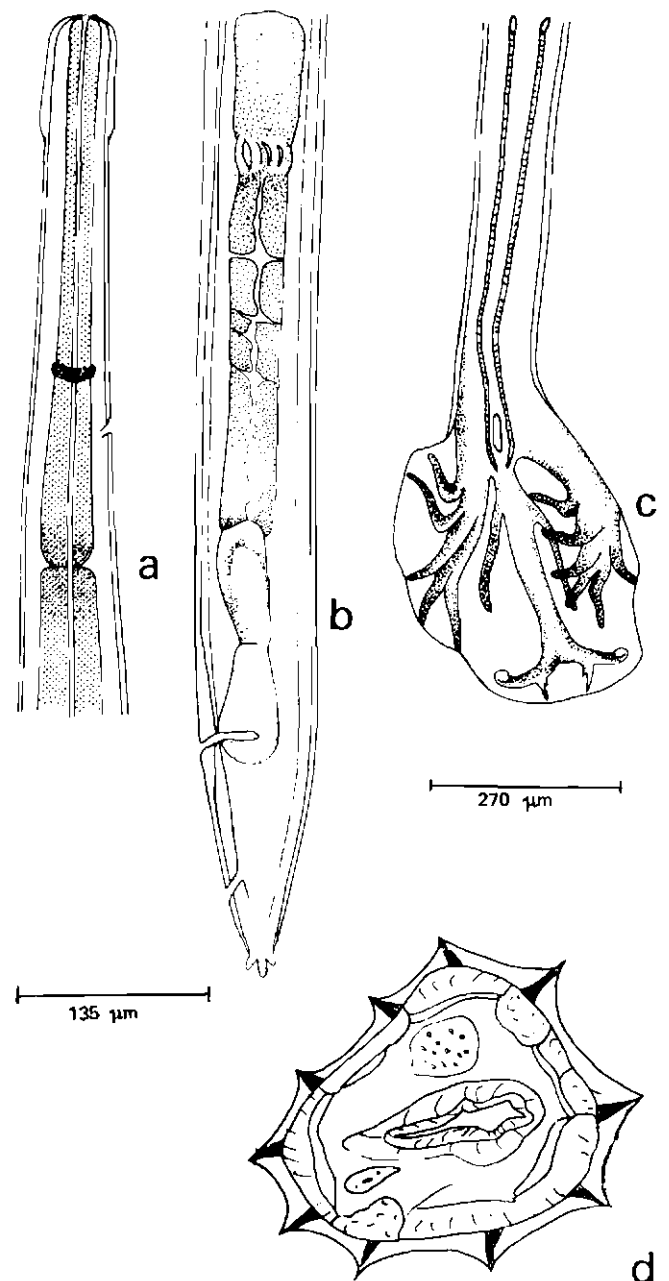


Figure 5 Fifth stage of *Impalaia tuberculata*: (a) Anterior end of female, (b) Posterior end and vulvar region of female, (c) Posterior end of male, (d) Cross section of male in the midbody region.

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Table 5 Dimensions of parasitic stages of *Longistrongylus sabie*

Sex	Male				Female					
	L4		5th		Early L4		Late L4		5th	
Stages of development	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Dimensions ^a										
Total length	2,2–4,1	3,5±0,6	4,5–6,7	5,4±0,9	1,6–5,3	3,5±1,5	3,7–7,4	5,1±1,0	5,3–8,4	6,6±1,0
Width: At anterior end	12–14	18,3±3,3	26–30	27,1±1,1	14–38	21,7±7,3	16–30	23,3±4,6	27–33	30,8±1,8
Across oesophagus	30–86	49,9±12,4	51–86	61,9±10,2	26–68	50,0±13,7	43–73	59,8±9,4	62–86	71,3±8,8
Maximum	38–86	60,1±15,2 ^b	68–108	82,4±12,6	30–81	53,0±21,3	46–92	77,6±14,2	70–135	96,9±18,2
At vulva	–	–	–	–	–	–	46–92	77,6±14,2	70–135	96,9±18,2
In front of bursa	–	–	68–104	81,6±11,2	–	–	–	–	–	–
At anus	–	–	–	–	17–32	25,1±5,3	25–35	30,8±3,2	32–49	41,2±4,6
Oesophagus: Length	311–562	452,7±86,3	528–665	559,9±41,7	227–534	371,1±124,7	443–626	551,3±54,8	520–632	584,6±28,5
Width at base	22–46	30,6±6,8	27–43	37,2±5,0	22–41	28,8±5,7	27–43	34,3±5,5	38–62	48,9±7,7
Distance from cervical papillae to anterior end	–	–	332–355	345,3±8,0	–	–	–	–	335–421	376,3±28,3
Distance from excretory pore to anterior end	189–395	281,9±60,4	260–325	290,9±20,8	209–300	253,5±31,0	247–373	298,5±42,4	303–355	322,1±17,8
Distance from nerve ring to anterior end	143–354	226,7±67,0	198–284	243,7±24,7	143–247	195,33±33,4	195–306	225,7±36,1	202–314	265,4±37,6
Genital primordium: Length	testes began to develop		–	–	203–248	222,2 ^c	–	–	–	–
Width	testes began to develop		–	–	15–18	16,4 ^c	–	–	–	–
Distance from genital primordium to tail	–	–	–	–	292–493	353,0 ^c	–	–	–	–
Length of ovjectors	–	–	–	–	–	–	189–449	297,4±87,2	216–314	267,1±33,8
Distance from vulvar opening to tail (mm)	–	–	–	–	–	–	621–1215	844,4±153,2	834–1441	1109,8±200,7
Distance from anus to tail	not visible anymore		–	–	68–140	104,±25,0	113–243	140,8±38,5	108–189	143,1±26,0
Length of spicule	–	–	151–176	158,3±10,8	–	–	–	–	–	–

^a All measurements are given in µm unless stated otherwise. ^b Only three worms measured. ^c Only five worms measured

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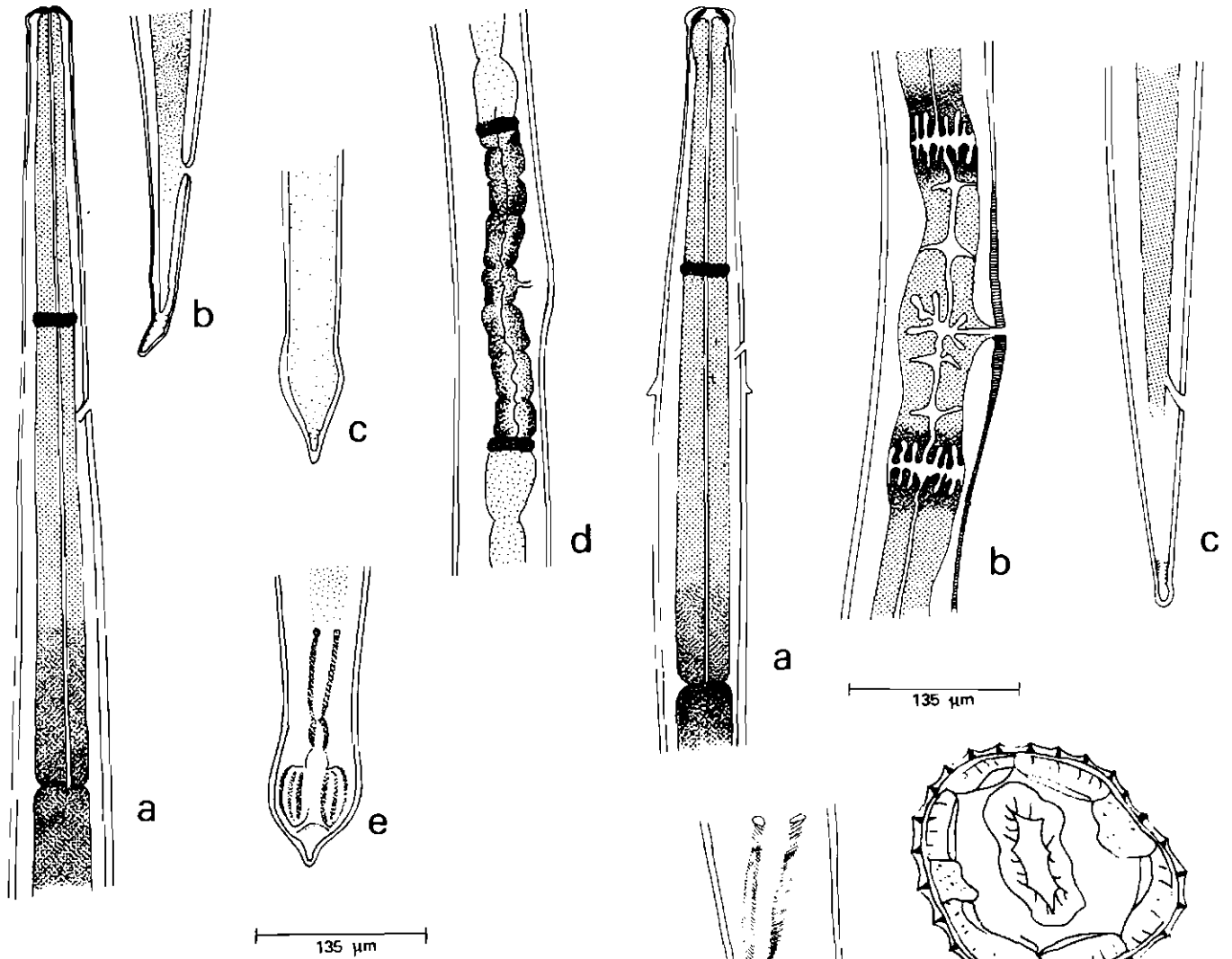


Figure 6 L4 of *Longistrongylus sabie*: (a) Anterior end of female, (b) Posterior end of female, (c) Posterior end of male, (d) Vulvar region of late L4, (e) 4th moult in male.

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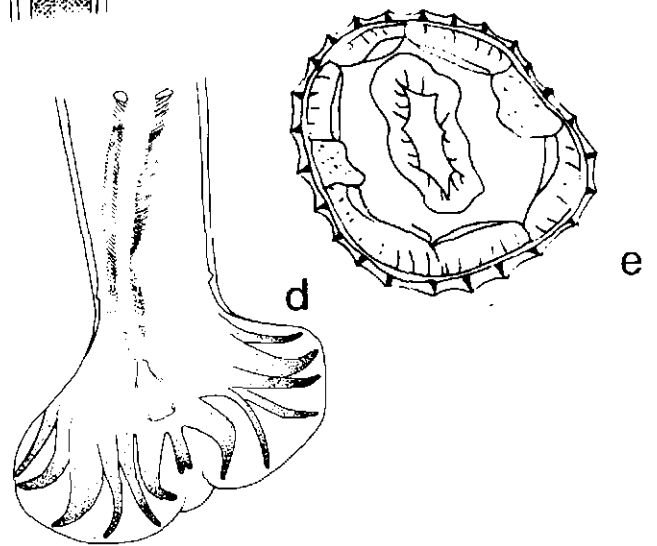


Figure 7 Fifth stage of *Longistrongylus sabie*: (a) Anterior end of female, (b) Vulvar region of female, (c) Posterior end of female, (d) Posterior end of male, (e) Cross section of male in the midbody region.