

OSWALDOFILARIA CHABAUDI N. SP. (NEMATODA: ONCHOCERCIDAE) FROM A SOUTH AMERICAN TROPIDURID LIZARD (SQUAMATA: IGUANIA) WITH AN UPDATE ON OSWALDOFILARIINAE

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Summary:

A new species of *Oswaldofilaria* is described from *Tropidurus torquatus* (Tropiduridae: Iguania); its prevalence at the rocky study area at Juiz de Fora, Minas Gerais, Brazil, was approximately 30 % and its mean intensity 3.13 ± 2.51 . *Oswaldofilaria chabaudi* n. sp. is distinct from the thirteen *Oswaldofilaria* species known in Australia, Africa and South-America in having the following characteristics: oesophagus medium-sized, left spicule 1 mm long and high spicular ratio (about 5), tail extremity ornated in both sexes with a bifurcated projection, and tooth-like structures near phasmids in the female. A long left spicule and high spicular ratio are convergent derived characters also found in a parasite of Australian crocodylians, *O. kanbaya*, and in several species of the closely related genus *Befilaria*, such as the Central American *B. puertoricensis* from polychrotids. *Oswaldofilaria* in South America is represented by eight species. Within these, a primitive group that is parasitic in Iguanidae, Polychrotidae (Iguania) and Crocodylidae and that possesses a long oesophagus is recognised, together with two distinct derived lines: three species with numerous, aligned precloacal papillae, parasitic in Teiidae (Laterata) and Scincidae (Scincomorpha), and *O. chabaudi* n. sp., in which this character is absent. Tropidurids (*Tropiduris* and *Plica*) had previously been reported in the host range of two oswaldofilarine genera, *Oswaldofilaria* and *Piratuba*, and their parasites assigned to known species described from other groups of lizards.

KEY WORDS: *Oswaldofilaria chabaudi* n. sp., Filarioidea, Onchocercidae, Oswaldofilarinae, *Tropidurus torquatus*, Squamata, Tropiduridae, Minas Gerais, Brazil.

Résumé: *OSWALDOFILARIA CHABAUDI* N. SP. (NEMATODA: ONCHOCERCIDAE) CHEZ UN LÉZARD SUD-AMÉRICAIN TROPIDURIDAE (SQUAMATA: IGUANIA) ET SYNTHÈSE SUR LES OSWALDOFILARIINAE

Une nouvelle espèce d'*Oswaldofilaria* est décrite chez *Tropidurus torquatus* (Tropiduridae : Iguania); la prévalence de la filaire est proche de 30 % et l'intensité moyenne de $3,13 \pm 2,51$ dans l'aire rocheuse de l'étude, Juiz de Fora, Minas Gerais, Brésil.

Oswaldofilaria chabaudi n. sp. est distinct des treize espèces d'*Oswaldofilaria* connues en Australie, Afrique et Amérique du Sud par l'oesophage de longueur moyenne, le spicule gauche long de 1 mm et le rapport spiculaire élevé (proche de 5), l'extrémité caudale ornée dans les deux sexes par une protubérance bifide, et les denticules près des phasmides chez la femelle. Le spicule gauche long et le rapport spiculaire élevé sont des caractères dérivés convergents, observés aussi chez un parasite de crocodile d'Australie, *O. kanbaya*, et chez plusieurs espèces du genre proche *Befilaria*, comme *B. puertoricensis* parasite de Polychrotidae en Amérique Centrale. *Oswaldofilaria* en Amérique du Sud est représenté par huit espèces parmi lesquelles sont identifiés un groupe primitif avec un oesophage long, parasite d'Iguanidae, Polychrotidae (Iguania) et Crocodylidae, et deux groupes évolués : trois espèces à nombreuses papilles précloacales alignées, parasites de Teiidae (Laterata) et Scincidae (Scincomorpha), et *O. chabaudi* n. sp. qui n'a pas ce caractère. Des Tropiduridae (*Tropidurus* et *Plica*) étaient déjà connus comme hôtes de deux genres d'Oswaldofilarinae, *Oswaldofilaria* et *Piratuba*, et leurs parasites identifiés à des espèces décrites dans d'autres groupes de lézards.

MOTS CLÉS : *Oswaldofilaria chabaudi* n. sp., Filarioidea, Onchocercidae, Oswaldofilarinae, *Tropidurus torquatus*, Squamata, Tropiduridae, Minas Gerais, Brésil.

INTRODUCTION

Among onchocercid filarial worms, the subfamily Oswaldofilarinae Chabaud & Choquet, 1953 is distinct in that the vulva is situated very far from the head (Chabaud & Choquet, 1953). A series of other characters suggests that it is not an artificial group: the developed glandular oesophagus, the presence of a buccal capsule, the absence of an *area rugosa* and a thick tail in the males, and large caudal papillae arranged in a cloacal and a terminal group (Bain, 1974; Anderson & Bain, 1976). The thirty-two species within the Oswaldofilarinae represent seven genera, two of which are monotypic (Bain *et al.*, 1982). All filariae from Crocodylia and a part of those from Sauria (lizards) belong

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to this subfamily. *Oswaldofilaria* Travassos, 1933 has a gondwanian-type geographical distribution and is represented by thirteen species, including the four parasitic in crocodylians (Travassos, 1933; Marinkelle, 1981; Bain *et al.*, 1982; Manzanell, 1986). *Befilaria* Chabaud, Anderson & Brygoo, 1959 comprises three species in the Ethiopian region (Chabaud *et al.*, 1959; Bain & Ranque, 1974; Gibbons, 1989) and one in the Neotropical region (Bain & Chaniotis, 1975). *Piratuboides* Bain & Sulahian, 1974 is present in South America and Australia only, with one and two species, respectively [the single African species is not a *Piratuboides* but a Splendidofilariinae, *Madathamugadia huambensis* (Petit, Bain, Gomes & Touratier, 1983) (Bain *et al.*, 1993)]. The remaining four genera have a restricted distribution. *Piratuba* Lent & Freitas, 1941 is represented in the Neotropical region by seven species, including the poorly-known *P. mitchelli* (Smith, 1910) (Smith, 1910; Lent & Freitas, 1941; Pelaez & Perez-Reyes, 1960; Chabaud & Frank, 1961; Bain, 1974). *Conispiculum* Pandit, Pandit & Iyer, 1929, revalidated by Bain *et al.* (1982) and represented by two species (Castellani & Willey, 1905; Pandit *et al.*, 1929; Baylis, 1939; Bain *et al.*, 1982), and the monotypic *Gonofilaria* Mullin, 1973 occur in India (Mullin, 1973). The single species of *Solafilaria* Chabaud, Anderson & Brygoo, 1959 is found in Madagascar (Chabaud *et al.*, 1959).

The host range of Oswaldofilariinae and the fact that all filarial species from crocodylians belong to this subfamily, have induced several comments on the probably remote origin of these filariae, with a suggested date as early as the late Jurassic (Bain *et al.*, 1982; Chabaud & Bain, 1994). It is also supposed that, since that date, they were transmitted by culicids, because the life cycles of modern representatives have all been obtained in mosquitoes: a species of *Conispiculum* in India (Pandit *et al.*, 1930) and five species of *Oswaldofilaria* from Australia (Mackerras, 1953) and South America (Prod'hon & Bain, 1972; Bain & Chabaud, 1975).

Besides the evolutionary interest of oswaldofilarines, estimation of their specific diversity is another interesting and delicate matter. In this paper we describe a new species found in a Tropicuridae, a family of Iguania already reported in the host range of two genera, *Oswaldofilaria* and *Piratuba*. The present finding contrasts with the picture resulting from the rather numerous surveys of oswaldofilarine species parasitising lizards that were conducted in South America. All materials observed during the past thirty years in Brazil (Vicente, 1981; Vicente *et al.*, 1993; Silva & Kohlsdorf, 2003), Paraguay (Burseley & Goldberg, 2004) and Peru (Burseley *et al.*, 2005) were assigned to known species. Furthermore, in the Neotropical region, the most recent description was that of a parasite from a crocodylid (Marinkelle, 1981).

MATERIAL AND METHODS

For a survey of its helminth fauna, the lizard *Tropidurus torquatus* (Wied-Neuwied, 1820) was trapped in an area of rocky outcrops in the vicinity of Toledos, Juiz de Fora, state of Minas Gerais, Brazil (21° 48' 27.5" S; 43° 35' 31.7" W). This area is characterized by rocky soils, shrubby vegetation and a seasonal climate with dry winters and wet summers. Tie and glue traps were used and captures were made from August 2005 to June 2007, during day light hours. Thirty-eight males (snout-vent length SVL 88.82 ± 21.23 ; range 51.2 – 127.2 mm) and 72 females (SVL 75.74 ± 13.62 ; range 42.1 – 101.4 mm) were trapped. Lizards were euthanized, the body cavity was opened by a longitudinal incision from vent to throat and the gastrointestinal tract and other organs were removed. Concerning the localization of the filariae in the lizards, 35 % were found in the body cavity, 65 % in the muscular aponeuroses, of which 58 % in the thighs (equally right and left) and 7 % at the basis of the tail.

Species and authority names follow the Craig Venter reptile database (Venter, 2009). Supra-generic divisions of iguanian lizards follow Frost *et al.* (2001a, b), while larger phyla in Squamata follow Hedges & Vidal (2009). Filarial worms were fixed in AFA (95 parts 70 % ethanol, 3 parts 40 % formalin, and 2 parts glacial acetic acid), stored in 70 % ethanol and cleared in lactophenol for examination. The anterior extremity was studied in apical view. The width of the lateral chord was measured in lateral view; attention was given to the presence and/or absence of deirids in several male and female specimens. For detailed studies, samples of microfilariae were extracted from the uterus near the ovijector; the ovijector and spicules were dissected out in one female and one male specimen, respectively. Buccal capsule length is the distance from oesophagus apex to mouth. Oesophagus ratio is oesophagus length/body length given in percent. Spicular ratio is length of left/right spicule. Vulva ratio is the distance vulva to apex/body length as a percentage. Specimens were drawn using a microscope equipped with a camera lucida. Measurements were made on drawings and are given in micrometers, except where otherwise stated.

DESCRIPTION

OSWALDOFILARIA CHABAUDI N. SP.

The study is based on 24 females and 24 males. Morphological characters are shown in Figs 1 and 2. Individual measurements of types and a few other specimens, including a young female and a young male, as well as ranges and means in females and males are presented in Table I.

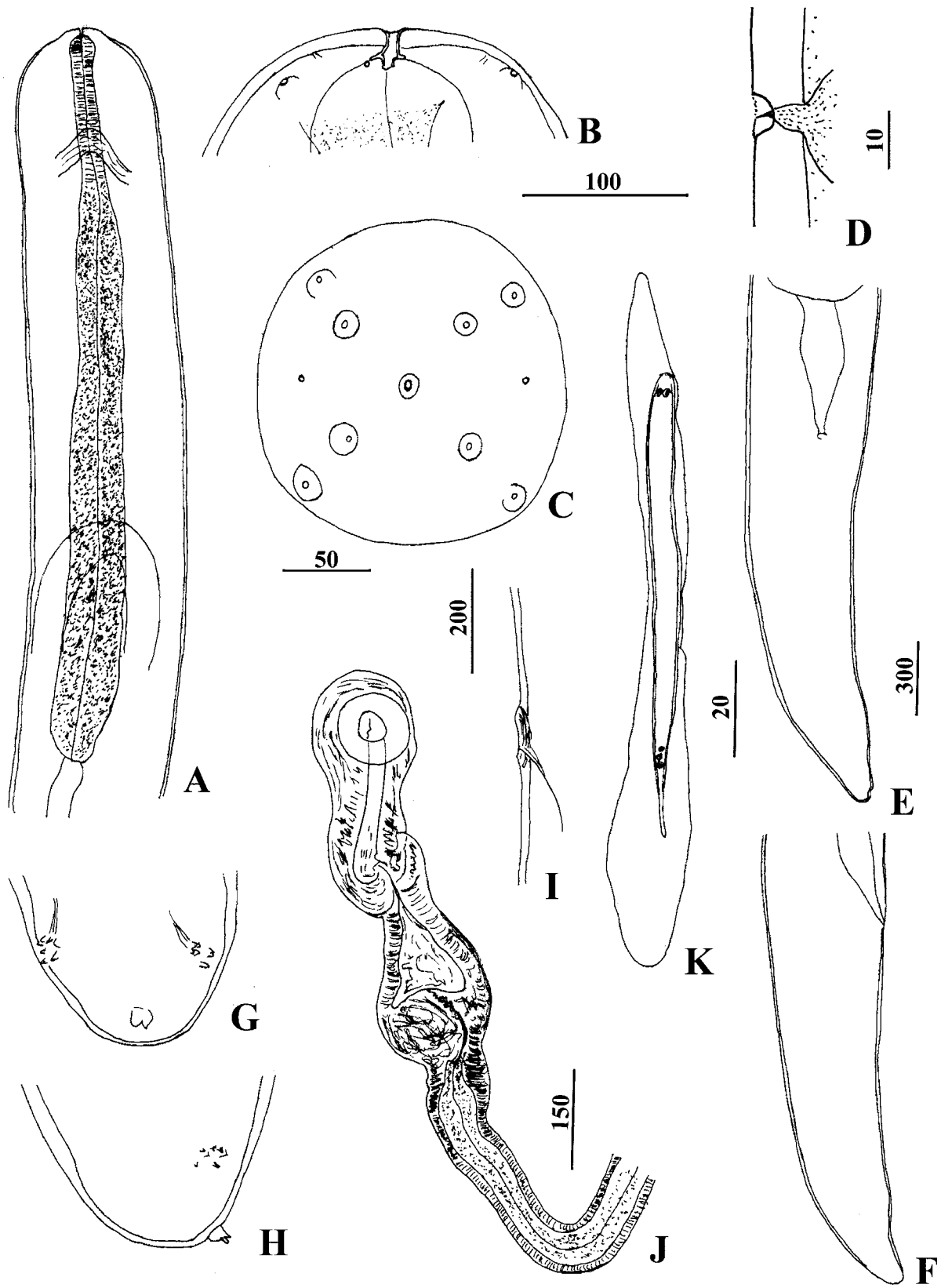


Fig. 1. – *Oswaldofilaria chabaudi* n. sp. from *Tropidurus torquatus*. Female. A. Anterior region, dorsoventral view (dotted line indicates extension of uteri). B. Head, lateral view, holotype. C. Head, in front view. D. Deirid, median view. E. & F. Tail in ventral and right lateral views. G & H. Caudal extremity in ventral and right lateral views. I. Vulva, lateral view. J. Vagina, ventral view. K. Microfilaria from uteri of a paratype. Scales in μm : A,E,F, 300; B,G,H, 100; C, 50; D, 10; I, 200; J, 150; K, 20.

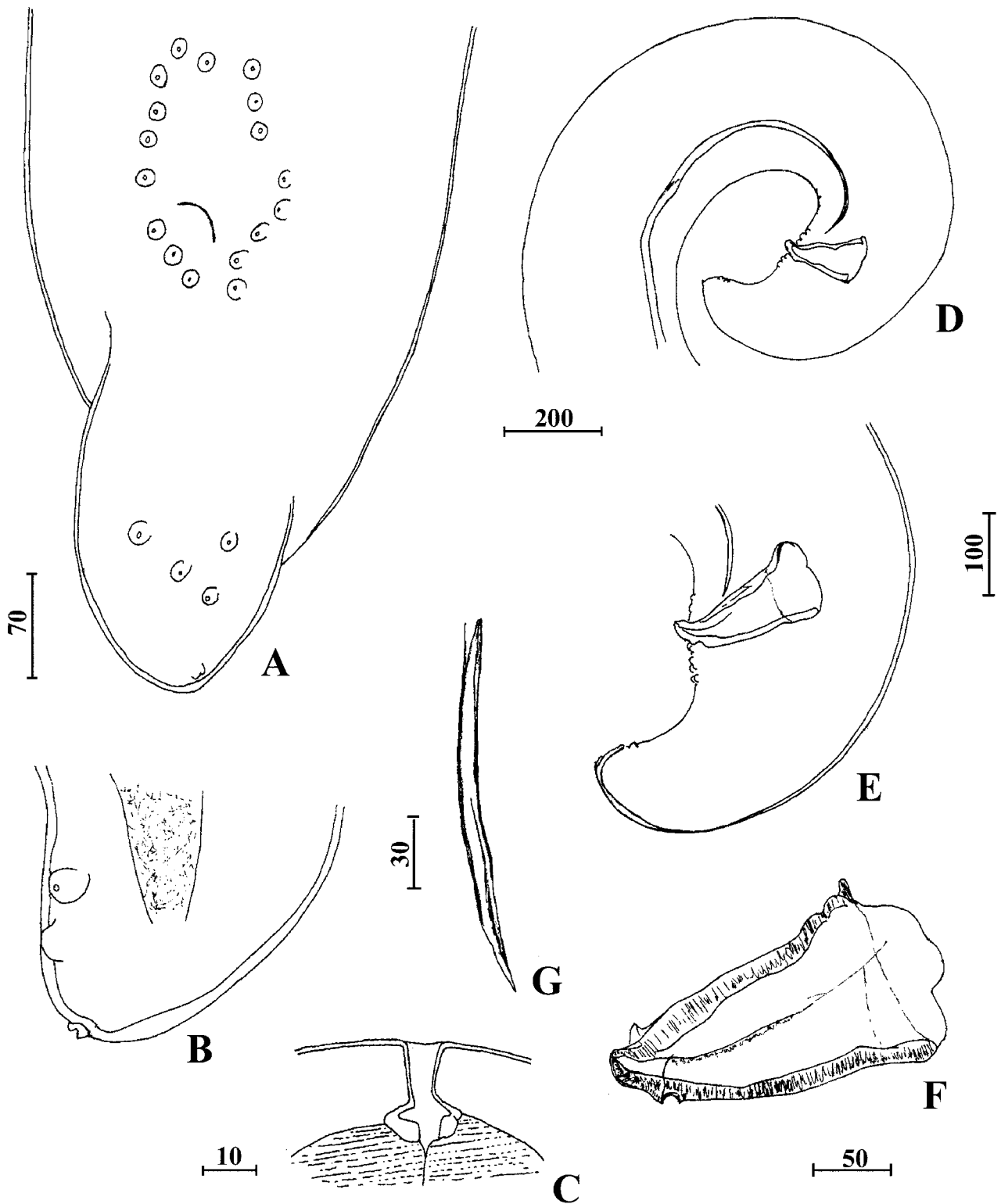


Fig. 2. – *Oswaldofilaria chabaudi* n. sp. from *Tropidurus torquatus*. Male. A. Tail, ventral view. B. Extremity of tail, left lateral view. C. Buccal capsule, lateral view, allotype. D. Posterior region and spicules, left lateral view. E. Tail, left lateral view. F. Right spicule, left lateral view. G. Distal extremity of left spicule, left lateral view. Scales in μm : A,B, 70; C, 10; D, 200; E, 100; F, 50; G, 30.

Type host: *Tropidurus torquatus* (Wied-Neuwied, 1820) (Tropiduridae: Iguania: Sauria), type host specimen III-1, deposited in “Coleção Herpetológica do Departamento de Zoologia da Universidade Federal de Juiz de Fora”, registration number 229.

Type locality: Toledo (21° 48' 27.5" S; 43° 35' 31.7" W), Juiz de Fora, Minas Gerais, Brazil.

Site: muscular aponeuroses of thighs and base of tail, body cavity.

Type material: female holotype, male allotype and female paratype 109YU; deposited in the Helminth collection of the Muséum National d'Histoire Naturelle (MNHN), Paris.

Other material: recovered from the same host species and locality. One female 102YU, one male 106YU (anterior part), one male and one female 107YU and one male 108YU, deposited in the Helminth collection of the MNHN, Paris. Other specimens preserved in the Laboratório de Taxonomia e Ecologia de Helmintos, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, Brazil. Prevalence and mean intensity: 29.1 % and 3.13 ± 2.51.

Body thick. Cuticle thin, slightly thicker laterally. Lateral chords wide, about one third of body width at mid-body.

Anterior region almost as thick as mid-body; extremity subround and, in some specimens, narrowed head (Fig. 1A). Head with four external labial and four cephalic sublateral papillae, arranged in two squares; amphids tiny (Fig. 1C). Buccal opening small and circular; buccal cavity small, with anterior narrow, thin-walled tube and posterior part shorter and wider, with thicker wall (Figs. 1B, 2C). Deirids tiny, identified in all specimens they were searched for, posterior to beginning of glandular oesophagus (Fig. 1D). Oesophagus clearly divided into short anterior muscular portion and long, thicker glandular portion (Fig. 1A); total oesophagus length shorter in males than females (mean 1,915 and 2,355, respectively), but ratio about three fold higher in males (11 % and 4.14 %, respectively; Table I).

In female, genital tract tightly coiled, the most anterior bend reaching level of nerve ring in the larger specimens. Vulva at end of anterior third of body, often on slightly salient plateau ornated with a few circular striae (Fig. 1I); in one specimen a few small scales present on plateau. Vagina large (300 long and 170 wide in holotype) and complex: two chambers separated by sphincter; second chamber more developed and separated from ovijector by strongly muscular sphincter (in holotype, chambers 110 and 160, respectively; Fig. 1J).

Female and identification number	Holotype 109 YU	Paratype 109 YU	102 YU	105 YU	Young 13.1	Mean (n = 23)	Range (n = 23)
Length (mm)	52	60	72	70.5	37	62.3	54.5-77.4
Width	500	500	510	650	390	490	430-640
Buccal capsule length	19	18	18	20	18	20	18-29
Nerve ring to head	425	390	410	430	340	400	380-490
Deirids to head	1,300 & 1,430	950 & 980	1,090 & 1,335	1,000 & ND	ND	ND	ND
Total length oesophagus	2,050	2,400	2,850	2,350	2,060	2,355	1,940-3,000
Oesophagus ratio (%)	3.9	4	3.9	3.3	5.5	4.14	3.2-5.5
Muscular oesophagus	350	400	620	510	310	430	300-620
Vulva to head (mm)	15.7	21.48	26.4	20.3	ND	23.82	19.33-27.06
Vulva ratio (%)	30.2	35.8	36.6	28.8	ND	34.8	28.8-40
Tail length	1,000	950	1,260	750	650	1,130	750-1,550
Male and identification number	Allotype 109 YU	106 YU	108 YU	Young 8.2	Mean (n = 23)	Range (n = 23)	
Length (mm)	14	ND	16	6.79	17.8	13.83-24.06	
Width	265	330	240	260	260	260-310	
Buccal capsule length	16	ND	17	20	15	10-20	
Nerve ring to head	260	250	270	200	220	160-270	
Deirids to head	600 & 600	710 & 790	700 & 960	ND	ND	ND	
Total length oesophagus	1,750	2,000	1,980	1,870	1,910	1,590-2,350	
Oesophagus ratio (%)	12.5	ND	12.3	27.5	11	8.8-13.3	
Muscular oesophagus	240	400	400	300	350	290-490	
Tail length	397	330	380	290	340	300-400	
Right spicule	180	200	240	210	200	190-240	
Left spicule	920	1,100	980	1,070	960	840-1,070	
Handle left spicule	350	250	250	ND	ND	ND	
Spicular ratio	5.1	5.5	4.1	5.1	4.7	4-5.15	

Table I. – Measurements of females and males of *Oswaldofilaria chabaudi* n. sp. from *Tropidurus torquatus*. Young specimens are not included in mean and range. ND: not determined.

Ovijector tubular, 80-90 wide and 1.8-1.94 mm long, (measured in seven specimens). Posterior body region narrower than anterior part. Tail long, thick and distinctly narrowed in distal region (Fig. 1E, F); phasmidial pores with 5-6 tiny, pointed, tooth-like structures; round extremity ornated with bifurcated projection (Fig. 1G, H).

In male, caudal region spirally coiled (one and half tight turns); thick, short, conical tail, extremity round with bifurcated terminal projection (Fig. 2A, B); *area rugosa* absent. Total number of caudal papillae: 19 to 22; arranged in two groups; anterior group composed of 7-8, more or less regularly placed pairs, of which 3 pairs are para- and postcloacal; posterior group composed of two subterminal pairs (Fig. 2A, B). Spicules distinctly unequal and dissimilar; right spicule short, stout, triangular in lateral view, with subterminal transverse circular crest (Fig. 2F); left spicule long, uniformly thin, slightly twisted between handle and lamina (Fig. 2D); distal region of lamina spiraled, with bevelled extremity (Fig. 2G).

Microfilaria short; head with small cephalic hook; thin, anucleated caudal extremity; sheath loose, longer than microfilaria, one extremity more attenuated (Fig. 1K). Measurements (n = 20, from paratype): body 90 (83-93) long, 8 (7-9) wide; cephalic space 8 long; last caudal nucleus 15 from posterior end.

Taxonomic discussion

A key to the genera of the *Oswaldofilariinae* was given by Bain *et al.* (1982) to complete the one published by Anderson & Bain (1976), which did not include *Conispiculum*. Our material is compared to the five genera that possess an ovijector with a complex vagina ("sphincter complexe"). Among these genera, *Conispiculum* and *Gonofilaria* are excluded because their spicules are subequal (ratio ≤ 1.3). *Solafilaria*, *Oswaldofilaria* and *Befilaria* have unequal spicules (ratio ≥ 2). *Solafilaria* is excluded because its vulva is close to the anus, whereas it is in the anterior mid-part of the body in the latter two genera. These are distinguished by the oesophagus length in females, > 2 mm in *Oswaldofilaria*, < 1 mm in *Befilaria* (Bain, 1974; Bain *et al.*, 1982). The present material has an oesophageal mean length of 2,355 in females, with a single measurement just under 2,000 (1,940), and is, therefore, placed in the genus *Oswaldofilaria*. It is, however, noted that, while the reference length given for the oesophagus in *Befilaria* applies well to the two Afromalagasy species (Chabaud *et al.*, 1959; Bain & Ranque, 1974), it does not comply with the remaining two species; particularly in females of *B. puertoricensis* Bain & Chaniotis, 1975 the oesophagus reaches 1,335 in length (Bain & Chaniotis, 1975). The validity of the closely related genera *Oswaldofilaria* and *Befilaria* is questionable.

The following thirteen species of *Oswaldofilaria* are currently recognized (Table II):

- In Australia five species: *O. kambaya* Manzanell, 1986 from a crocodile (*Crocodylus porosus* Schneider, 1801), the others from two species of Agamidae, *O. chlamydosauri* (Breinl, 1913) (type-host *Chlamydosaurus kingii* Gray, 1825), *O. innisfailensis* (Mackerras, 1962), *O. pflugfelderi* (Frank, 1964) (both transferred in the genus by Bain & Sulahian, 1974), *O. samfordensis* Manzanell, 1982 [type-host of the last three species is *Physignatus lesueurii* (Gray, 1831)].

- In Africa *O. versterae* Bain, Kouyaté & Baker, 1982 from *Cr. niloticus* Laurenti, 1768.

- In South America seven species: one Colombian, *O. medemi* Marinkelle, 1981 from a crocodile [*Paleosuchus trigonatus* (Schneider, 1801)]; six Brazilian species, *O. bacillaris* (Molin, 1858) also from a crocodile (*Caiman crocodilus* Linnaeus, 1758); *O. brevicaudata* (Rodhain & Vuylsteke, 1937) from an iguanid [*Iguana iguana* (Linnaeus, 1758)], *O. azevedoi* Bain, 1974 from a polychrotid [type-host *Polychrus marmoratus* (Linnaeus, 1758)]; two species from teiids, *O. petersi* Bain & Sulahian, 1974 [type-host *Tupinambis teguixin* (Linnaeus, 1758)], *O. belemensis* Bain & Sulahian, 1974 (type-host *Dracaena guianensis* Daudin, 1802); and *O. spinosa* Bain & Sulahian, 1974 from a scincid [type-host *Mabuya mabouya* (Bonnaterre, 1789)]. All these species (Table II) are distinct from the present material by many characters, of which only the most obvious are reported below.

As a general remark on the species of *Oswaldofilaria*, the oesophagus is longer, rarely equal but never shorter in females than in males, and the oesophagus ratio is higher in males, rarely equal in both sexes (Table II).

Six species are distinct from the new species in having a longer oesophagus. In *O. versterae*, it is 4,730 long in the male and the oesophagus ratio is 16.3 % *vs* 1,590-2,350 long and 8.8-13.3 % in our material; no data are available on the female. In *O. bacillaris* (redescribed by Prod'hon & Bain, 1972), *O. medemi*, *O. kambaya*, *O. brevicaudata* (redescribed by Bain & Sulahian, 1974) and *O. azevedoi*, the oesophagus is $\geq 3,340$ in the female and the ratio $\geq 10\%$ (not known in *O. azevedoi*) *vs* 1,940-3,000 long and ratio 3.2-5.5 % in our females; in the male of these species the oesophagus is $\geq 2,400$. These species also have a tail length < 500 in the female. In addition, in the first four species, which are parasitic in crocodiles, no more than three to four pairs of pre- and para-cloacal papillae are present and these are regularly aligned; the spicular ratio does not exceed 4, except in *O. kambaya*. Other distinctive characters are listed for each species: *O. versterae* has a twice longer right spicule than the present material (Bain *et al.*, 1982); in *O. bacillaris* the mouth and buccal capsule are oriented dorsally (Prod'hon & Bain, 1972); *O. medemi* has the longest oesophagus (13,000 in females, 6,100 in males),

the tip of its left spicule is lanceolated, the right spicule is twice shorter than in *O. chabaudi*, and the tip of the tail is smooth in both sexes (Marinkelle, 1981); *O. kanbaya* has two phasmidial conical lappets in the tail of both females and males, a right spicule without a sub-terminal crest and a round extremity, as well as longer microfilariae (170 vs 83-93) (Manzanell, 1986); *O. brevicaudata* has no spines, or projections on the tail in both sexes and the microfilaria is 140-160 long; in *O. azevedoi* the distal extremity of the left spicule is a folded membrane (Bain, 1974).

In the remaining seven species the oesophagus length and ratio is similar to our specimens. However, their spicular ratio does not exceed 3. The *Oswaldofilaria chlamydosauri* female (redescribed by Manzanell, 1982), has a long tail (700) as seen in our specimens, but the male possesses a distinctly attenuated tail, a gubernaculum, and the left spicule has a membranous extremity; the buccal cavity is flattened laterally and deirids are absent in both sexes. In the other species, the female tail does not exceed 550. *Oswaldofilaria petersi*, *O. belemensis* and *O. spinosa* have several additional pairs of regularly aligned pre-cloacal papillae; head papillae are arranged in a laterally stretched rectangle; in addition, in the first two species, the body cuticle is ornated with transverse bands of longitudinal crests, whereas the female tail of the third species has two terminal cushions covered with points (Bain & Sulahian, 1974). *Oswaldofilaria samfordensis* is large, with a long buccal capsule, 40 to 100 (mean 50) in females and 30 in males (Manzanell, 1982). In *O. pflugfelderi*, of which the specific validity was confirmed by Manzanell (1982), the tail extremity of both sexes is devoid of spines or projections, and the microfilariae are longer (150 vs 83-93), with a tight sheath and refringent granules (Frank, 1964). *Oswaldofilaria innisfailensis* is unique in that its vulva is slightly posterior to the oesophageal-intestinal junction (3.9 mm from head, vulva ratio 5 %; Mackerras, 1962) and microfilariae are 126 long (Manzanell, 1982). Finally, none of the known *Oswaldofilaria* species have a vagina that is composed of two chambers.

We conclude that the material parasitic in *Tropidurus torquatus* from Brazil is a new species, *Oswaldofilaria chabaudi*, named in honour of Alain Gabriel Chabaud for his dedication to science and his invaluable scientific contribution to the field of Helminthology.

GENERAL DISCUSSION

The new species, *O. chabaudi* n. sp., is easily characterized by the caudal bifurcated projection in both sexes, the long female tail, bearing tooth-like structures near the phasmids, the thin left spicule that is about 1 mm long, a spicular ratio ranging from

4 to 5.15, a vagina with two chambers, and a middle-sized oesophagus.

When considering the affinities of the new species, it is seen that *O. kanbaya*, a parasite of Crocodylidae in Australia, also has a long, thin left spicule and a spicular ratio of 5, as do several species of *Befilaria*, including the Neotropical representative, *B. puertoricensis*. These similarities seem to result from homoplasy, because *O. kanbaya* possesses a long oesophagus, *Befilaria* a short one and that of *O. chabaudi* n. sp. is of intermediate size. In filarioid nematodes, a phyletic value is given to oesophagus dimensions: a large oesophagus with a well-developed glandular part is a primitive character that is observed in all infective larvae of Onchocercidae (cf Bain & Chabaud, 1986). In the infective larvae of *Oswaldofilaria*, the oesophagus ratio ranges from 32 to 59 %; later, in the host, there is a tendency to reduce the digestive tract, linked to the tissular habitat of these parasites, and a short oesophagus is considered a derived character. *Befilaria* is very close to *Oswaldofilaria*, but is retained because of the smaller oesophagus size; however, the length limit is $\leq 1,400$ in females instead of 1,000 as reported previously (Bain *et al.*, 1982). In the genus *Oswaldofilaria*, species parasitic in Crocodylidae from Africa (Bain *et al.*, 1982), South America (Travassos, 1933; Marinkelle, 1981) and Australia (Manzanell, 1986) all have a long oesophagus and can be considered primitive (Table II).

In Australia, as underlined by Manzanell (1986), the single *Oswaldofilaria* from a crocodile is well distinct from the four species parasitic in Agamidae. The male oesophagus of the latter is less than 2,500 long, and some of them have additional derived characters, such as the laterally flattened buccal capsule and a gubernaculum in *O. chlamydosauri*; the left spicule is transformed into a tube in the distal half in *O. samfordensis* (cf. Manzanell, 1982), and in *O. innisfailensis* the vulva is anterior. This is not the case in South America, where two species from iguanid and polychrotid lizards, *O. brevicaudata* and *O. azevedoi*, respectively, have a long oesophagus, deirids, head papillae that are arranged in a square, and cannot be opposed to species parasitic in crocodiles. This resemblance, which contrasts with the host groups, suggested that *Oswaldofilaria* had diversified at an epoch when Saurians and Crocodylidae were both present and not geographically dispersed, that is before the break-up of Gondwana, about 150 MY ago (Hedges & Vidal, 2009). Indeed, the infective larvae of *Oswaldofilaria* spp. from a crocodile and from diverse lizards have a very peculiar character in common, which is the presence of longitudinal cuticular crests on their body (Bain & Chabaud, 1986).

Considering the present data, the Neotropical region displays the highest diversity of *Oswaldofilaria* parasitic in Sauria (Vicente *et al.*, 1993; Silva & Kohlsdorf, 2003;

<i>Oswaldofilaria species</i>	<i>chabaudi</i>	<i>bacillaris</i>	<i>versterae</i>	<i>kanbaya</i>	<i>medemi</i>	<i>brevicaudata</i>		
Authority parasite name	n. sp.	(Molin, 1858)	Bain, Kouyaté & Baker, 1982	Manzanell, 1986	Marinkelle, 1981	(Rodhain & Vuylsteke, 1937)		
Female	Holotype	°	*	Type	Allotype	Allotype	**	***
Length (mm)	52	45	64	X	31	49	37.6-42.8	17.3
Width at mid-body	500	250	375	510	250	250	447-500	270
Buccal capsule length	19	15	14	X	20	16	16	6
Nerve ring to head	425	600	330	X	ND	425		240
Deirids to head	1,300 & 1,430	ND	1,250	X	absent	?		absent
Oesophagus length	2,050	9,000	4,800	X	3,500	13,000	4,140-4,220	3,340
Oesophagus ratio (%)	3.9	30	10	X	11.2	26.5	9.8-11.1	19.3
Muscular oesophagus	350	1,000	ND	X	500	535	456-560	290
Vulva to head (mm)	15.7	13-21	12.8	X	9.2	16.8	12.7	6.6
Vulva ratio (%)	30.1	28	20	X	29	34	33	38
Tail length	1,000	350	435	300	320	296	352-408	395
Male	Allotype	°	*	Type	Holotype	Holotype	**	***
Length (mm)	14	20	31.8	29	18	24	16-18	6.6
Width	265	210	310	240	150	200	171-210	150
Buccal capsule length	16	8	10	15	15	12	16	ND
Nerve ring to head	260	360	525	250	350 ¹	298		
Deirids to head	600	ND	875	600	absent	?		
Oesophagus length	1,750	5,300	3,585	4,730	3,200	6,100	2,810-3,210	2,400
Oesophagus ratio (%)	12.5	26.5	11.25	16.3	17.7	25.4	17.5	36.6
Muscular oesophagus	240	650	575	330	400	238	367-436	ND
Tail length	397	140	265	330	180	154	160-200	160
Right spicule	180	180	160	450	110	92	136-160	135
Left spicule	920	380	450	870	550	366	296-312	220
Spicular ratio (left/right)	5.1	2.1	2.8	1.93	5	3.9	1.95	1.7
Microfilaria²		°	*				**	***
Length	89-93	ND	84-117	95-102	170	86-92	ND	140-160
Width	7-9	ND	6-9	6	6.5-7	5.3-5.4	ND	7
Host genus	<i>Tropidurus</i>	<i>Caiman</i>	<i>Crocodylus</i>	<i>Crocodylus</i>	<i>Crocodylus</i>	<i>Paleosuchus</i>	<i>Iguana</i>	
Host species	<i>torquatus</i>	<i>crocodilus</i>	<i>niloticus</i>	<i>porosus</i>	<i>trigonatus</i>	<i>iguana</i>		
Authority host name	(Wied- Neuwied, 1820)	Linnaeus, 1758	Laurenti, 1768	Schneider, 1801	(Schneider, 1801)	(Linnaeus, 1758)		
Host family	Tropiduridae	Crocodylidae	Crocodylidae	Crocodylidae	Crocodylidae	Iguanidae		
Country	Brazil	Brazil	Africa	Australia	Colombia	Brazil		
Main location in host	Aponeuroses, body cavity	Aponeuroses	ND	Peritoneum	Thoracic wall	Dorsal peritoneum		

° In Travassos (1933). * In Prod'hon & Bain (1972). ** In Freitas & Lent (1937). *** In Bain (1974) (measurements of Rodhain & Vuylsteke are close to those of Bain and not reported). **** In Manzanell (1982). ND: not determined. X: not measurable because worm not complete. ?: not searched. ¹: measured on the figure.

²: From blood or uterus; ND: not determined.

Table II. – The fourteen species of *Oswaldofilaria*, including *O. chabaudi* n. sp. Species are presented according to the order used in the discussion. Unless otherwise specified, the authorities of parasite names match the reference.

<i>azevedoi</i>	<i>spinosa</i>	<i>petersi</i>	<i>belemensis</i>	<i>pflugfelderi</i>	<i>innisfailensis</i>	<i>cblamydosauri</i>	<i>samfordensis</i>
Bain, 1974	Bain & Sulahian, 1974	Bain & Sulahian, 1974	Bain & Sulahian, 1974	(Frank, 1964)	(Mackerras, 1962)	(Breinl, 1913)	Manzanell, 1982
Type	Type	Type	Type	Paratype (range)	A female	**** (range)	Allotype (range)
X	34	64	115	77	68	64	121
520	380	450	450	500	330	450	560
ND	13	17	25	15	ND	50 (25-50)	50 (40-100)
760	220	380	350	420	ND	5,501	4,001
1,160 & 1,570	absent	?	?	?	?	absent	present
3,720	2,300	2,500	2,300	2,800	2,600	2,300	2,600
X	6.9	4	2	4.5	3.8	3.6	2.1
800	340	480	360	580	600	700	600
15.8	16.6	15.6	27	18	3.9	25.6	43.56
X	48	24	23	25 (23-38)	5	40	36
490	340	260	480	550	390	700	520
Type	Type	Type	Type	Holotype	A male		Holotype
21.5	16.5	26.2	63	27	20	29	52
290	230	260	375	255	230	320	370
13	12	17	20	25	ND	18	30
420	270	300	320	380	ND	310	
805 & 870	absent	?	?		?	absent	present
2,400	1,140	1,750	2,310	1,774	1,770	2,000	2,000
11.2	7	7	3.6	6.5	8.8	6.8	3.8
410	280	380	380	374	350	500	500
250	260	160	260	120	210	320	360
190	98	90	180	115	155	140	170
400	298	380	465	280	320	260	370
2.1	3.1	3.1	2.58	2.4	2	1.8	2.1
180-192	58	58-62	68-78	150	126***	110-122	83
7	4	9	9/9.5	ND	ND	6.5	7.7
<i>Polychrus marmoratus</i>	<i>Mabuya mabouya</i>	<i>Tupinambis teguixin</i>	<i>Dracaena guianensis</i>	<i>Physignatus lesueurii</i>	<i>Physignatus lesueurii</i>	<i>Cblamydosaurus kingii</i>	<i>Physignatus lesueurii</i>
(Linnaeus, 1758)	(Bonnaterre, 1789)	(Linnaeus, 1758)	Daudin, 1802	(Gray, 1831)	(Gray, 1831)	Gray, 1825	(Gray, 1831)
Polychrotidae Brazil	Scincidae Brazil	Teiidae Brazil	Teiidae Brazil	Agamidae Australia	Agamidae Australia	Agamidae Australia	Agamidae Australia
Body cavity	Armpit, spinal aponeuroses	Peritoneum Intestinal wall	Heart & large vessels	Aponeuroses	Subperitoneal tissue	Peritoneum Aponeuroses	Peritoneum Aponeuroses

Burseley & Goldberg, 2004; Bursey *et al.*, 2005). The six *Oswaldofilaria* species represent three morphological groups which are not related to the host groups. These are in Iguania, the primitive *O. brevicaudata* and *O. azevedoi*, parasitic in Iguanidae and Polychrotidae, respectively; the derived *O. chabaudi* n. sp. from Tropiduridae; in other Sauria, the three last species with distinct derived characters (numerous and aligned precloacal papillae, head papillae arranged in a rectangle), *Oswaldofilaria spinosa* parasitic in Scincidae (Scincomorpha), *O. petersi* and *O. belemensis* from Teiidae (Laterata),

When taking only the original descriptions into account, the absence of congruence between host groups and parasite species appears obvious among the South American *Oswaldofilaria* spp. This is reinforced when further reports are referred to. To take a recent example, the host range and geographic distribution of two species that were originally found in the Amazonian region of Belem, Para, Brazil, have been extended: *O. azevedoi* described from *Polychrus marmoratus* (Polychrotidae) was reported from a tropidurid, *Plica umbra* Linnaeus, 1758, in the western part of the Amazonian basin in Peru, at Reserva Cuzco Amazonica (Bursey *et al.*, 2005); *O. petersi*, described from the teiid *Tupinambis teguixin*, was reported in *Tropidurus hispidus* Spix, 1825 in Bahia, Brazil (Silva & Kohlsdorf, 2003), but in this case the identification seems doubtful, because the typical numerous precloacal, aligned papillae are not figured and a gubernaculum is reported.

Parasite host lists are considerable work and of great importance in extending our knowledge on the distribution of nematodes. However, recent studies on diverse groups, such as Rhabdiasidae from lizards (Lhermitte-Vallarino *et al.*, 2009) and anurans (Junker *et al.*, 2010), as well as Seuratidae (Lhermitte-Vallarino *et al.*, 2007) or trichostongylids (Durette-Desset, 2006) from lizards suggest that species identifications should be taken with caution. In the case of filariae, the microfilaria is an important discriminative character (Esslinger, 1987, to cite only one example), the study of which is, however, often omitted. The exact degree of diversity is difficult to estimate, but in general it proved to be higher than expected and, in the cited recent works, morphological and molecular analyses were congruent when both were performed. Consequently host specificity and the notion of generalist parasites attributed sometimes to parasites of cold-blooded hosts (Bursey *et al.*, 2005) are difficult to assess.

Since the prevalence of *O. chabaudi* n. sp. is close to 30 % in *T. torquatus*, a common lizard in Juiz de Fora area, it seems possible to further the investigation on this oswaldofilarine, by elucidating its life cycle and larval morphology; we expect a culicid vector and an infective larva with longitudinal crests. The species is

also important when considering mutualistic relationships with the endobacterial *Wolbachia* and its evolutionary history (Casiraghi *et al.*, 2005; Fenn *et al.*, 2006). Interestingly, to date, the few filarial species from Lissamphibians and Squamata that have been studied do not harbour *Wolbachia* (Casiraghi *et al.*, 2004; Bain *et al.*, 2008), contrary to many species parasitic in mammals. It should be noted, however, that *Wolbachia* presence was investigated in a single Oswaldofilariinae only, belonging to the genus *Pirartuba*.

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