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Systematic and distribution of *Orihelia anticlava* (Molin, 1858) (Nematoda, Onchocercidae) from dasypodids of South America

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Abstract

Among the Dasypodidae (Xenarthra), 5 species are currently known to be hosts of *Orihelia anticlava* (Molin, 1858) in Brazil, Paraguay and Argentina. We gather all the information regarding taxonomy, morphology, ecology and geographical distribution of *O. anticlava*, in order to hypothesize on the origin and evolution of this filaria which is parasitic in an interesting host group, Dasypodidae. An amount of 192 specimens of 9 species of dasypodids from Argentina were prospected. *Chaetophractus villosus* and *Tolypeutes matacus* were parasitized. Measurements are provided, and the area rugosa described. Uterine microfilariae of *O. anticlava* show a considerable range of sizes; length of blood microfilariae seem not to be affected by geography; and, blood microfilariae are bigger than uterine ones. Despite that this parasite occurs in different host species, adults worms studied so far were morphologically alike. Prevalence and mean intensity were: *C. villosus* 10.8% and 8.5, *T. matacus* 3.7% and 1. Taking into account the geographic distribution of the hosts and the phylogeny of the dasypodids, we suggest that *O. anticlava* could be more widespread than currently noticed and other genera of dasypodids, such as *Cabassous*, *Chlamyphorus*, and *Zaedyus*, could also be parasitized. We believe that central Argentina, Uruguay, southern and northeastern Brazil should be considered preferable prospecting areas.

Key words

Orihelia anticlava, Filarioidea, Nematoda, Dasypodidae, Argentina

Introduction

The Xenarthra is constituted by the common named anteaters (Myrmecophagidae), armadillos (Dasypodidae) and sloths (Bradypodidae and Choloepidae), confined to the Neotropics and the adjoining temperate latitudes of South and North America (Wetzel 1982). They are apparently the most primitive members within the eutherians. The group evolved in South America in the Paleocene and later spread through the continent to get the current distribution (Engelmann 1985).

Twelve species of filarioids were reported to parasitize Xenarthra:

From Dirofilariinae: *Bostrichodera spiralis* (Molin, 1860) and *B. becquaerti* (Sandground, 1938), with primitives features; *Dirofilaria freitasi* (Machado de Mondonça, 1948), *D. incrassata* (Molin, 1858), *D. macrodemos* (Eberhard, 1978), and *D. panamensis* (Eberhard, 1978) with derived features; all parasites of sloths (Bain *et al*. 1983).

From Onchocercinae: *Acanthocheilonema sabanicolae* Eberhard and Campo-Aasen, 1986; *Strianema venezuelensis* Eberhard, Orihel and Campo-Aasen, 1993; *Orihelia anticlava* (Molin, 1858), with primitives features, and the derived species *Dasypafilaria averyi* (Eberhard, 1982), all of them parasites of armadillos; and 2 parasites of sloths and anteaters: *Chabfilaria freistaslenti* (Yeh, 1957) and *C. jonathani* Bain, Purnomo and Dedet, 1983 (Bain *et al*. 1983, Eberhard and Campo-Aasen 1986).

Orihelia anticlava parasitize several species within the Dasypodidae from South America and inhabits the body cavity of its hosts. It has a buccal capsule composed of two segments well cuticularized, cephalic plate laterally elongated, oesophagus divided into muscular and glandular regions, an asymmetrically distributed caudal papillae of the male, gubernaculum present, and caudal lappets in both sexes (Lent and Freitas 1942, Chabaud and Bain 1976). It is a primitive species within the *Dipetalonema* line, and a paleoendemic genus in South America (Chabaud and Bain 1976). Together with *Skrjabinofilaria* Travassos, 1925, a parasite of marsupials, both genera constitute the more primitive filarioids of the Onchocercinae in this continent (Bain *et al*. 1982). It seems

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that the ancestor of *Orihelia* speciated by the capture phenomenon, after the separation of Gondwana (upper Cretaceous), following the appearance and diversification of new host species (i.e., the Xenarthra). Later, the diversification processes of the nematodes stopped, and these parasites suffered little morphological change since then (Chabaud and Bain 1976).

The literature regarding *O. anticlava* is scarce, fragmentary, and to a considerable extent, controversial. We aimed to gather all the available information regarding the taxonomy, morphology, ecology and geographical distribution of *O. anticlava*, in order to hypothesize on the origin and evolution of this filaria which is parasitic in an interesting host group, Dasypodidae.

Materials and methods

From 1978 to 2000, 192 specimens of dasypodids were received from several localities of the provinces of Formosa, Chaco, Santiago del Estero, Córdoba, Santa Fé, Corrientes, Mendoza, La Pampa, Buenos Aires and Santa Cruz (Fig. 1), and their viscera were collected. Adult worms were recovered from the abdominal cavity, fixed in AFA or 10% formalin and preserved in 70% ethanol. Filarioids were cleared in lactophenol and observed under light microscope (LM) and measured with a graduate ocular lent. For scanning electron microscopy (SEM), specimens were dehydrated in ethanol series, dried with the critical point technique, and coated with gold. We used a JEOL JSM T100 electron microscopy. Microfilariae were obtained from the uteri of fixed mature females. We also examined microfilariae from *O. anticlava* deposited at Museum National d'Histoire Naturelle (MNHM) Paris (gift from Oswaldo Cruz, collected by Travassos 1940, identify by Freitas 1941). Blood samples from live-trapped host were taken from: 4 *C. villosus* (Jacinto Arauz, La Pampa province), cultivated in a 96 hours lymphocytes culture MEN (minimum essential medium GIBCO) with 10% bovine fetal serum and the smears stained with hematoxylin and eosin; and 20 *C. villosus* (Bahía Blanca, Buenos Aires province) and the smears stained with Giemsa. For prevalence and mean intensity terms we follow Bush *et al.* (1997), for nomenclature of the hosts to Wetzel (1982), and for distribution of the hosts to Eisenberg (1989), Redford and Eisenberg (1992), and Eisenberg and Redford (1999).

Results

Taxonomy

The list below are synonyms of *Orihelia anticlava* (Molin, 1858) Bain, Baker et Chabaud, 1982:

Filaria anticlava Molin, 1858; pp. 381, 450 (in Lent and Freitas 1942),

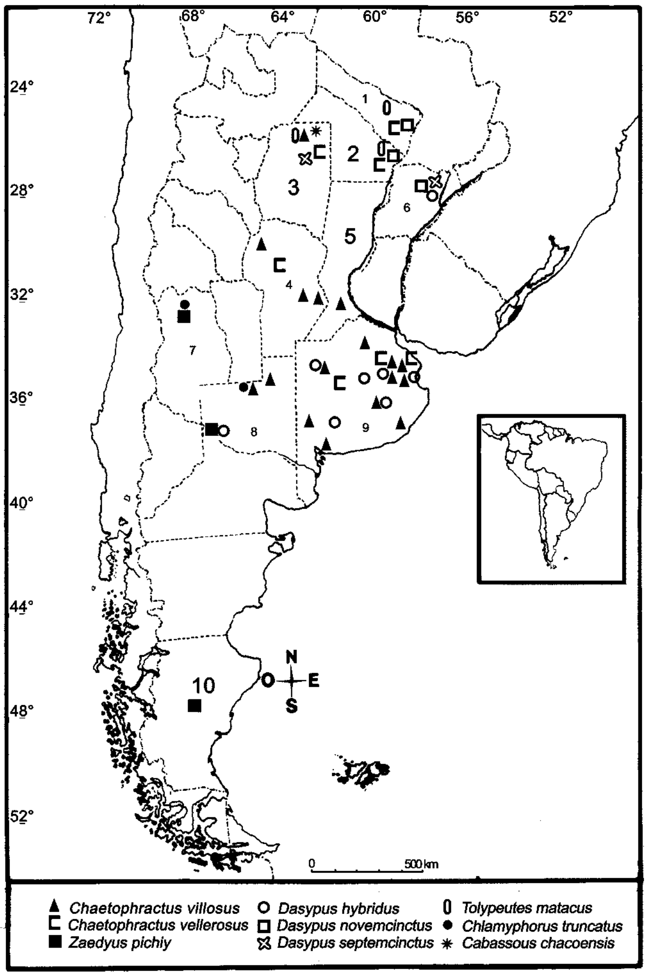


Fig. 1. Map of Argentina showing the localities where the dasypodids were trapped. Provinces: **1** – Formosa, **2** – Chaco, **3** – Santiago del Estero, **4** – Córdoba, **5** – Santa Fé, **6** – Corrientes, **7** – Mendoza, **8** – La Pampa, **9** – Buenos Aires, **10** – Santa Cruz

Filaria (*Dasypodis*) *gilvipedis* M. C. V. in Molin, 1858; p. 381 (in Lent and Freitas 1942),

Filaria anticlava Linstow, 1878; p. 62 (in Lent and Freitas 1942),

Filaria anticlava Stossich, 1897; p. 59 (in Lent and Freitas 1942),

Acanthocheilonema tatusi Mazza et Anderson, 1925; pp. 761–765 (in Lent and Freitas 1942),

Acanthocheilonema tatusi Mazza et Anderson, 1926; pp. 344–347 (in Lent and Freitas 1942),

Acanthocheilonema tatusi Mazza, Romaña et Fiora, 1932; pp. 993–996 (in Lent and Freitas 1942),

Setaria sp. Travassos, Freitas et Lent, 1939; p. 226 (in Lent and Freitas 1942),

Dipetalonema anticlava Lent et Freitas, 1942; pp. 275–280 (in Bain *et al.* 1982),

Dipetalonema anticlava Masi Pallares, 1970; pp. 27–34 (in Bain *et al.* 1982),

Dipetalonema (*Orihelia*) *anticlava* Chabaud et Bain, 1976; pp. 365–397 (in Bain *et al*. 1982),
Dipetalonema (*Orihelia) anticlava* Navone, 1990; pp. 199–210,
Dipetalonema anticlava Vicente, Rodrigues, Gomes et Pinto, 1997; p. 167.

Morphology

In Table I are shown the measurements obtained from 10 males and 10 females on *C. villosus* from Bahía Blanca (Buenos Aires), and those given by Lent and Freitas (1942) and Masi Pallares (1970). Specimens were deposited in the Helminthological Collection of Museo de La Plata CHMLP no. 4939 (4 males and 4 females); no. 4940 (1 male and 1 female SEM specimens), La Plata, Argentina.

Specimens of the genus *Orihelia* display a buccal capsule strongly cuticularized. In apical view under LM and SEM are observed the 4 labial and 4 cephalic papillae placed in a cephalic plate laterally elongated (Figs. 2 and 6–8). At SEM, the cuticle of the cephalic extremity is slightly striated, bulky amphids with a transverse aperture, cephalic papillae bigger and more protruded than the labial papillae (Fig. 3). The oesophagus is divided in an anterior muscular portion and a slightly wider glandular portion. The vulva placed a little posterior to the mid-length of the oesophagus (Fig. 9). In cross-section at the level of the vulva, lateral chords are broad, internal cuticular ridge rounded (Fig. 10). The tail has large cone-shaped lappets in both sexes (Fig. 4). The distributions of the cloacal papillae in the male are similar as Lent and Freitas (1942) and Masi Pallares (1970) described (Fig. 12). Under LM and SEM we have observed the ventral area rugosa in the male, which was not previously described. The area rugosa begins anterior to the cloaca and extends 3,516 (2,480–5,040) µm long. It is composed of transversal ridges (separate each one 25 µm) with small longitudinal crest of 1.4–3.5 µm (Figs. 5 and 13). The left spicule has a handle shorter than the distal filament (Fig. 14). Right spicule with a distal hook (Figs. 15–17). The mean spicular ratio is 3.02.

Microfilariae sheathed, body fusiform, tail rounded and nucleated (Fig. 11).

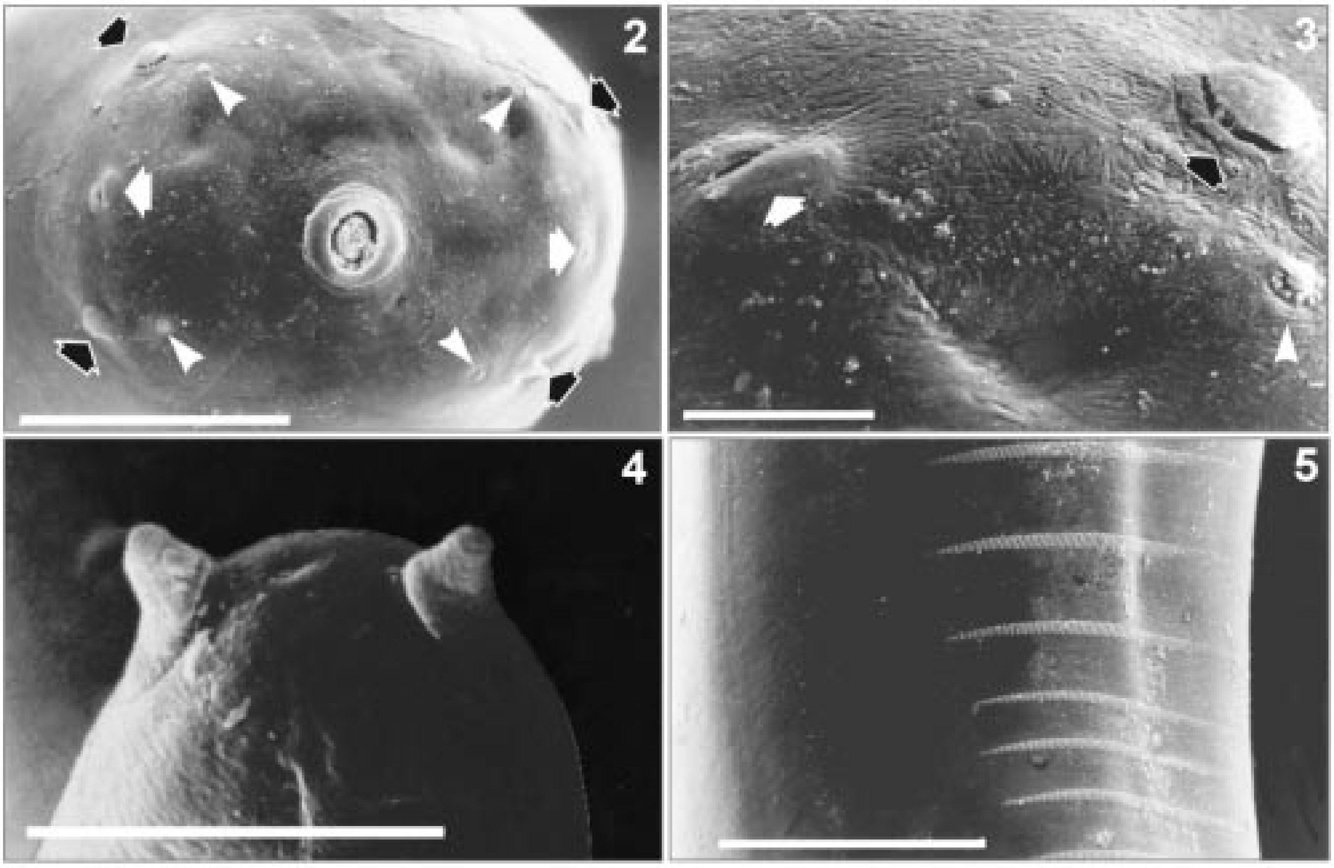
Uterine microfilariae: from *C. villosus* (locality: Pampa de los Guanacos, Santiago del Estero, Argentina), n = 9: length 76.05 (62–79), width 4.75 (4.5–5.5); from *E. sexcinctus* (locality: Salobra, Brazil) 689TW coll. MNHM Paris, n = 9: length 74.72 (69–79), width 4.61 (4.4–5).

Blood microfilariae from 5 upon 20 *C. villosus* (locality: Bahía Blanca, Buenos Aires) CHMLP no. 5099 stained with

Table I. Comparative measurements of *Orihelia anticlava*

		Lent and Freitas (1942)	Masi Pallares (1970)	Present study
Males	body length	25.79–28.14 mm	26–32 mm	31 (27.8–33.96) mm
	body width	230–250	300–400	236.89 (208–260)
	buccal capsule length	13	13–15	16.13 (14–20)
	buccal capsule width	19–20	18–21	21.22 (20–24)
	oesophagus length	1580–2700	1600–2400	1926.11 (1640–2180)
	oe. muscular length	330–410	–	439 (320–820)
	nerve ring	165–174	160–170	340 (300–380)
	tail	130–150	130–170	156.5 (136–180)
	left spicule	440–520	450–600	458.5 (340–560)
	right spicule	140–160	140–170	153 (140–180)
	gubernaculum	50–63	55–69	48.83 (40–56)
	area rugosa	–	–	3516 (2480–5040)
Females	body length	47.9–60.3 mm	48–70 mm	61.39 (57.92–65.2) mm
	body width	400–470	420–480	531 (465–564)
	buccal capsule length	13–17	15–18	16 (12–20)
	buccal capsule wide	21–25	21–25	22.60 (20–24)
	oesophagus length	1960–2160	2000–2430	1988.1 (1840–2200)
	oe. muscular length	360–430	420–440	380 (280–460)
	nerve ring	299–304	300–330	395.9 (348–432)
	tail	200–250	220–350	286 (260–320)
	vulva	870–1610	900–1420	1215 (1000–1408)
	ovijector	2870	2900	2710 (2320–3320)
Uterine microfilariae	length	50–59	60–70	76.05 (62–79)
	width	4	4	4.75 (4.5–5.5)
Host		*E. sexcinctus*, *D. novemcinctus*	*E. sexcinctus*	*C. villosus*
Locality		Data 2 to 8	Data 9	Data 12 (Bahía Blanca)

All measurements are in micrometers; amicrofilariae from *C. villosus* data 14 on Table II. See Table II for detailed data about the localities.



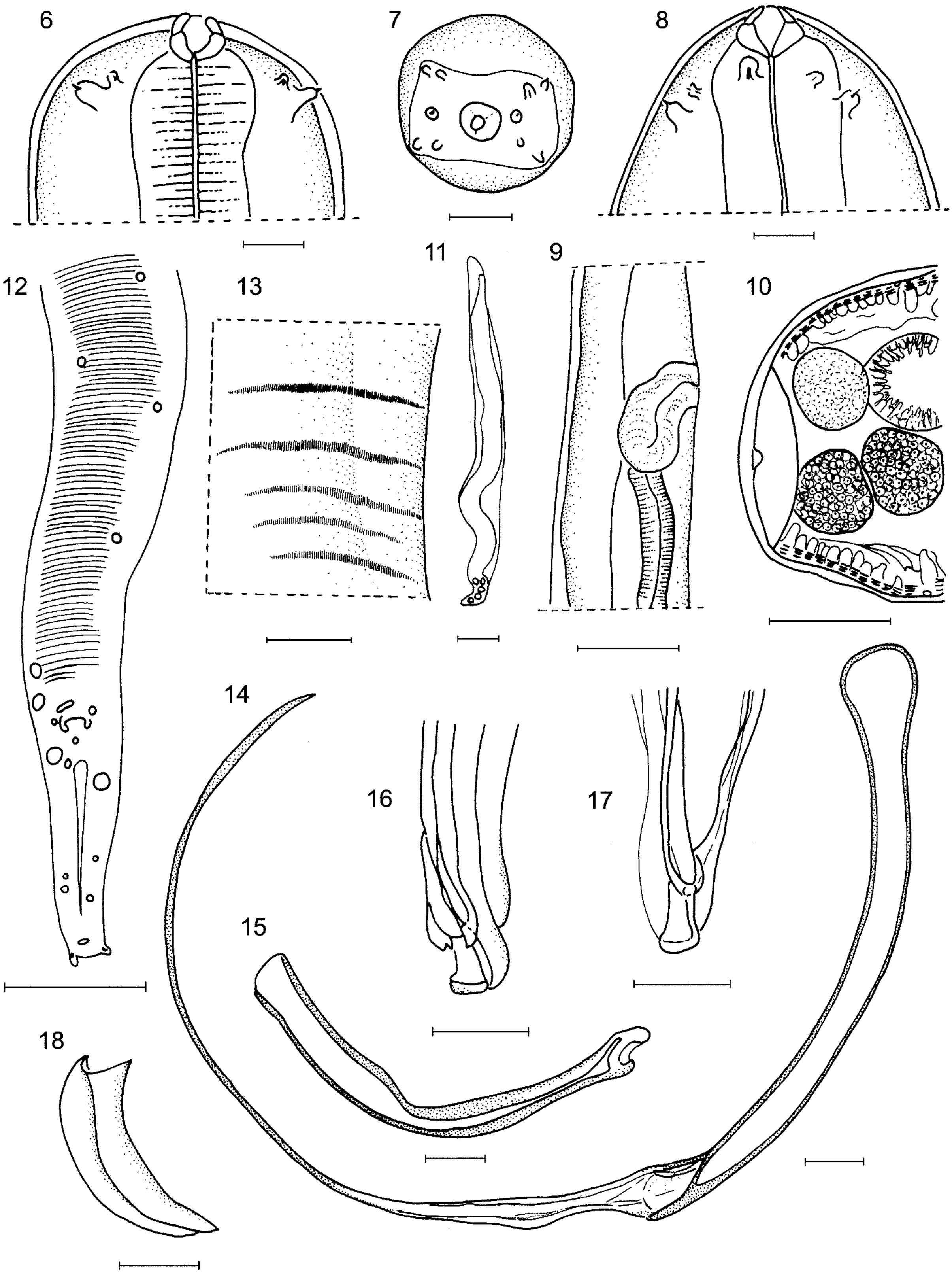
Figs. 2–**5.** *Orihelia anticlava*: **2** – apical view of the female showing amphids (thick white arrows), cephalic (black arrows) and labial papillae (small white arrows); **3** – detail of the amphids, cephalic and labial papillae; **4** – posterior extremity of the female showing the lappets; **5** – area rugosa of the male. Scale bars = 50 µm (2 and 5), 10 µm (3) and 33 µm (4)

Giemsa, n = 7: 90.71 (86–95) long, 4.71 (4–5) wide; from 4 *C. villosus* (locality: Jacinto Arauz, La Pampa) CHMLP no. 4941 in a lymphocytes culture, n = 7: length 90.71 (88–100), width 3.71 (3–4); sheath 103.1 (92–120) long and 9.1 (5–11) wide.

Ecology

The dasypodids trapped in the present study belonged to the following species: *Chaetophractus villosus* (Desmarest) (n = 74), *Ch. vellerosus* (Gray) (n = 12), *Tolypeutes matacus* (Desmarest) (n = 32), *Dasypus hybridus* (Desmarest) (n = 28), *D. novemcinctus* Linnaeus (n = 19), *D. septemcinctus* Linnaeus (n = 7), *Zaedyus pichiy* (Desmarest) (n = 15), *Chlamyphorus truncatus* Harlan (n = 4), and *Cabassous chacoensis* Wetzel (n = 1) (Fig. 1). Five specimens of *C. villosus* from Buenos Aires upon 61 (Chascomús, Bahía Blanca and Goyena), 2 from La Pampa upon 5 (Caleufú and Realicó), 1 from Santiago del Estero upon 2 (Pampa de los Guanacos), and 1 *T. matacus* from Santiago del Estero upon 27 (Pampa de los Guanacos) were parasitized with *O. anticlava*, harboring an amount of 69 worms. Thus, the mean intensities were 8.5 in *C. villosus* and 1 in *T. matacus*. The prevalence in *C. villosus* was 10.8% and 3.7% in *T. matacus*. No worms were found in the remaining dasypodids sampled. The intermediate host of this filarioid is still unknown. Ecological data are scarce and little can be derived from previous works (cf. Mazza and Anderson 1925, Masi Pallares 1970, Navone 1990). However, the present study provides the first data on prevalence and mean intensity.

Five species of dasypodids are currently known to be hosts of *O. anticlava*. It was originally described as a parasite of *Euphractus sexcinctus* Linnaeus by Molin (1858) (= *Dasypus gilvipes* Illiger), and collected by Natterer. Later, it was found in the same host by Travassos *et al*. (1939) (= *Dasypus setosus* Wied), Lent and Freitas (1942), Mazza *et al*. (1932) and Masi Pallares (1970); in *T. matacus* by Mazza *et al*. (1932) and Navone (1990); in *C. vellerosus* by Mazza *et al*. (1932); in *D. novemcinctus* by Lent and Freitas (1942); and in *C. villosus* by Navone (1990). Noteworthy is that several of the previous authors treated the hosts at the subspecies level (i.e. *E. sexcinctus tucumanus* and *C. vellerosus vellerosus*), however we consider this inconvenient because the taxonomic status of several of them is still uncertain (Carlini, pers. comm.).



Figs. 6–18. *Orihelia anticlava*: **6–8** – anterior end of the male, median, apical and lateral views; **9** – vulva; **10** – cross-section of the female, posterior to the vulva; **11** – blood microfilariae stained with Giemsa; **12** – tail of the male, ventral view; **13** – area rugosa at midlength; **14** – left spicule; **15** – right spicule, lateral view; **16** and **17** – distal extremity of right spicule, latero-dorsal and ventral views; **18** – gubernaculum. Scale bars = 20 µm (6, 8 and 14–18), 50 µm (7), 200 µm (9), 100 µm (10 and 12), 10 µm (11) and 25 µm (13)

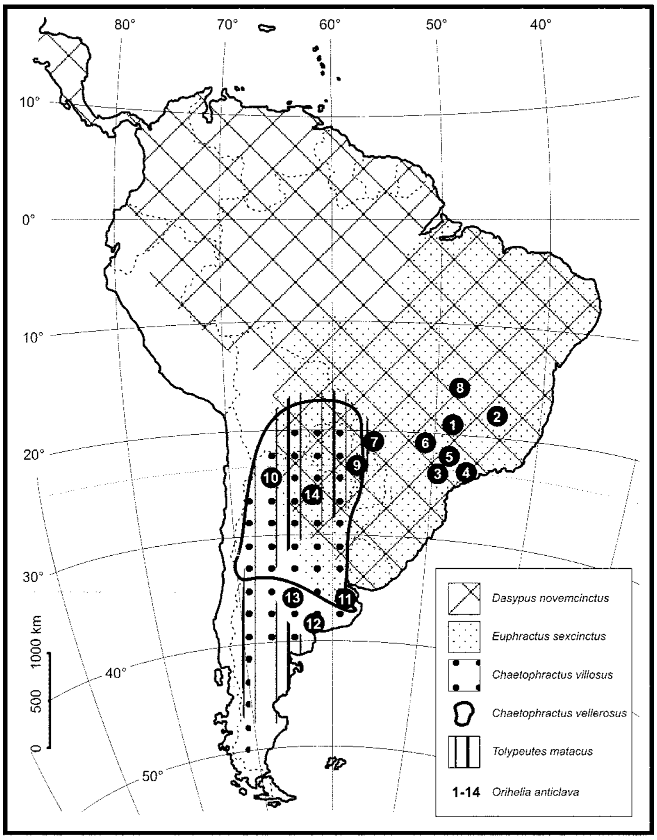


Fig. 19. Localities of *Orihelia anticlava* (black dots numbered from 1 to14), and geonemy of the 5 hosts species parasitized by this filarioid in South America. See also Table II for detailed data about the localities of *O. anticlava*

Distribution: Positive localities of *O. anticlava* against the geonemy of its currently known host are shown on Figure 19. In Table II are detailed each positive locality, the host and author that consigned the data. The type locality is Indianopolis (= Aldeia de Santana), Minas Gerais, Brazil. It was also mentioned for the States of Mato Grosso, São Paulo, Mina Gerais, and Distrito Federal (Travassos *et al*. 1939, Lent and Freitas 1942). In Paraguay, from Concepción (Masi Pallares 1970), and in Argentina from Jujuy (Mazza 1925), Buenos Aires and Santiago del Estero provinces (Navone 1990). In this work, we extend the distribution of *O. anticlava* to the province of La Pampa.

Discussion

Orihelia anticlava is a monotypic genus. Bain *et al*. (1983) were wrong when they refereed 2 *Orihelia* spp. in dasypodids (Bain, pers. comm.). The measurements and morphological features observed in our specimens are similar to those described by other authors. There are, however, some differences concerning the size of the microfilariae. The measures given by Lent and Freitas (1942) do not overlap with those we took from the same lot of microfilariae (*E. sexcinctus*; Salobra, Brazil) (50–59 vs 69–78). Moreover, Masi Pallares (1970) found that uterine microfilariae (in *E. sexcinctus*; Paraguay) ranged from 60 to70 µm, and thus filling the gap between the measurements taken by Lent and Freitas and ours. These findings suggest a considerable range of variation in the measurements of uterine microfilariae (50–78 µm).

Measurements of blood microfilariae, from *C. villosus* from different localities, overlapped in range (88–100 from La

Table II. Detailed data on the localities where *Orihelia anticlava* was found

	Locality name	Coordinates	State/Province	Country	Host species	Authors
1	Aldeia da Santanaa	19°S, 48°W	Minas Gerais	Brazil	*E. sexcinctus*	Molin 1858
2	Lassanse	17°53´S, 44°34´W	Minas Gerais	Brazil	*E. sexcinctus*	Lent and Freitas 1942
3	Itaporanga	17°15´S, 37°57´W	São Paulo	Brazil	*D. novemcinctus*	Lent and Freitas 1942
4	São Paulo Capital	23°35´S, 46°43´W	São Paulo	Brazil	*E. sexcinctus*	Lent and Freitas 1942
5	Jau	22°17´S, 48°33´W	São Paulo	Brazil	*E. sexcinctus*	Lent and Freitas 1942
6	Lussanvirab	20°40´S, 51°07´W	São Paulo	Brazil	*E. sexcinctus*	Lent and Freitas 1942
7	Salobra	20°50´S, 56°53´W	Minas Gerais	Brazil	*E. sexcinctus*	Travassos *et al*. 1939, Lent and Freitas 1942
8	Distrito Federal	~15°43´S 47°43´W		Brazil	*E. sexcinctus*	Lent and Freitas 1942
9	Rincón	~23°S, 57°W	Concepción	Paraguay	*E. sexcinctus*	Masi Pallares 1970
10	Perico	24°23´S, 65°06´W	Jujuy	Argentina	*E. sexcinctus, T. matacus, C. vellerosus*	Mazza and Anderson 1925, Mazza *et al*. 1932
11	Chascomús	35°34´S, 58°01´W	Buenos Aires	Argentina	*C. villosus*	Navone 1990
12	Bahía Blanca	38°43´S, 62°16´W	Buenos Aires	Argentina	*C. villosus*	Present study
	Goyena	37°43´S, 62°36´W	Buenos Aires	Argentina	*C. villosus*	Present study
13	Caleufú	35°34´S, 64°33´W	La Pampa	Argentina	*C. villosus*	Present study
	Realicó	35°01´S, 64°15´W	La Pampa	Argentina	*C. villosus*	Present study
14	Pampa de los Guanacos	26°14´S, 61°49´W	Santiago del Estero	Argentina	*T. matacus*, *C. villosus*	Navone 1990, Present study

1–14 – Dots on Figure 19 showing the positive localities of *Orihelia anticlava*; acurrently know as Indianopolis, bidem Pereira Barreto.

Pampa, 86–95 from Buenos Aires) and showed no statistical differences. This could indicate that geography affect only mildly in morphological variability of microfilariae.

We found that blood microfilariae, again from *C. villosus* and from different localities, were larger than uterine ones ($p<0.0001$). Based on similar morphological traits (i.e. tail rounded and nucleated), we ascribed them to the same parasitic species. This growth could comprise cellular enlargement rather than true development.

In sum, uterine microfilariae of *O. anticlava* show a considerable range of sizes; length of blood microfilariae seems not to be affected by geography; and, blood microfilariae are bigger than uterine ones. The biological meanings of these facts are yet to be explained.

Despite that *O. anticlava* parasite several host species, adult worms studied up to present day were morphologically alike. In turn, Bain and Durette-Desset (1973) observed that specimens of *Skrjabinofilaria* found in 5 species of marsupials were quite heterogeneous.

In their catalogue of nematodes from Brazil, Vicente *et al*. (1997), listed *D. novemcinctus*, *E. sexcinctus*, *E. sexcinctus tucumanus*, *T. matacus* and *C. vellerosus vellerosus* as host of *O. anticlava*, but the last three dasypodids mentioned above, are hosts cited for Argentina (Mazza *et al*. 1932). Moreover, *T. matacus* and *C. vellerosus* do not occur in Brazil. Vicente *et al*. (1997) refers only to Lent and Freitas (1942), but these last authors listed together the host species for Brazil and Argentina; thus, we consider that Vicente *et al*. (1997) were wrong. Only *D. novemcinctus* and *E. sexcinctus* are known to be host of *O. anticlava* in Brazil.

It is observable a disjoint distribution of *O. anticlava*: (1) a wide region between the 16°S and 26°S, from the eastern coast of Brazil to northwest Argentina (Fig. 19), and (2) a central region in Argentina. The 5 species of Dasypodidae parasitized by *O. anticlava* overlap in their geographic distribution in north-central Argentina (Fig. 19). The host with the largest distribution is *D. novemcinctus*, ranging from Argentina (south to the provinces of Santiago del Estero, Santa Fe, and Entre Ríos) to southern United States. *Euphractus sexcinctus*, distributed in the savannas of Brazil, Uruguay, Paraguay, and Argentina (south to Buenos Aires) is the next considering its range size (Eisenberg 1989, Redford and Eisenberg 1992, Eisenberg and Redford 1999). Taking into account the geographic distribution of the 5 dasypodids, we suggest that *O. anticlava* could be more widespread than currently noticed. In this sense, we suggest 2 areas of high importance that should be sampled in order to assess the pattern of the geonemy of *O. anticlava*. The first one consists of central Argentina, Uruguay, and south of Brazil; the other one is north-eastern Brazil (see Fig. 19). To sample these areas would allow us to face questions such as whether *O. anticlava* occurs in the grasslands of central Argentina, northern Uruguay, and southern extreme of Brazil; and whether or not it is also an Amazonian species. In this respect, it is interesting that Thoisy *et al*. (2000) found unidentified microfilariae in blood samples of *D. novemcinctus* and *D. kappleri* from French Guiana. As

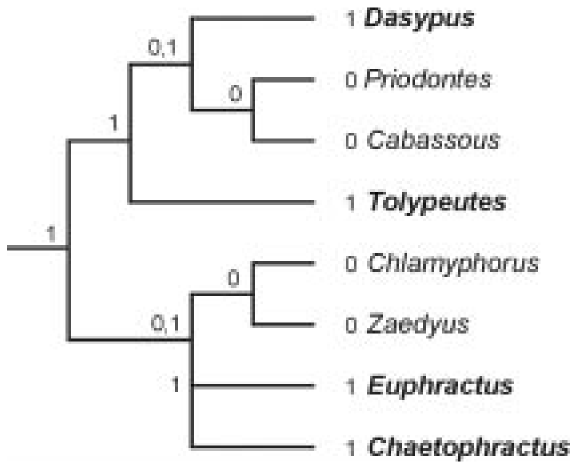


Fig. 20. Phylogeny of the Cingulata showing the character assignments for *Orihelia anticlava* (0 = absent, 1 = present)

D. novemcinctus is parasitized by *Dasypafilaria averyi* in North America (Eberhard 1982), and by *O. anticlava* in South America, French Guianan filarioids offer a good opportunity to clarify the distribution, and perhaps the phylogenetic relationship between *Orihelia* and *Dasypafilaria*.

From an evolutionary point of view, if Engelman's (1985) cladogram of the Cingulata (Fig. 20) describes the actual phylogenetic story of these mammals, *Orihelia* probably speciated in ancient dasypodids as it is present in quite distant taxa such as *Euphractus* and *Dasypus*. Being this so, we would expect that intermediate taxa such as *Cabassous*, *Chlamyphorus* or *Zaedyus*, would be also parasitized. Given the topology of the tree, the absence of *O. anticlava* in any of these taxa will not deny the ancient infestation theory because it is the most parsimonious choice.

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