

# The importance of host ecology in thelastomatoid (Nematoda: Oxyurida) host specificity

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## Abstract

An experimental investigation of host specificity within the Thelastomatoidea is presented by means of a comparison of the thelastomatoids of two panesthiine cockroaches, *Panesthia cribrata* and *P. tryoni tryoni*, with those of other log-dwelling arthropods and those of leaf litter dwelling arthropods found near by. 145 log-dwelling and leaf-litter dwelling arthropods, representing adjacent ecological niches, were collected from Lamington National Park, Queensland, Australia. A high degree of thelastomatoid species sharing (19 incidences from 26 specimens) occurs between log-dwelling arthropods and the two cockroach species. No overlap in thelastomatoid fauna was observed between the log dwelling and leaf-litter dwelling groups. Our results suggest that host specificity of thelastomatoids is largely dictated by host ecology.

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## 1. Introduction

Oxyurida (pinworms) are found in the hindgut of numerous vertebrates and invertebrates. They are transmitted directly by an infective egg, and have a haplodiploid lifecycle in which haploid males arise from unfertilized eggs and diploid females arise from fertilized eggs [1]. The oxyuridans are divided into two superfamilies, Oxyuroidea, which are pinworms found in vertebrates and Thelastomatoidea, pinworms of invertebrates, primarily terrestrial arthropods. Numerous studies [2–4], have shown a high degree of host specificity in oxyurids of primates. Additionally, Adamson and Nasher [5,6] have demonstrated a high degree of host specificity in oxyurids of agamid lizards.

Very little is known about specificity in the thelastomatoids, with the exception of that inferred by Adamson [7] from the collective reportings of this group in the literature, which suggested that host specificity in the Thelastomatoidea is highly variable. Four of the five families appear to be highly host specific: the Hystriognathidae are only found in passalid beetles,

the Protrelloididae are only found in cockroaches, the Pseudonymidae are only found in hydrophyilid beetles, and the Travassosinematidae are primarily found in mole crickets [8–10]. In contrast, the Thelastomatidae have been reported from beetles, cockroaches, flies, millipedes, mole crickets, one arachnid and one oligochaete, suggesting much lower levels of specificity occur in this family [8]. However, Adamson [7] acknowledged that “there is little direct experimental data demonstrating the ability of pinworms to infect hosts other than their natural ones.”

To date only one study of the Thelastomatoidea has directly examined the degree of parasite sharing between host species [11]. This study compared the parasite fauna of two closely-related wood-feeding panesthiine cockroaches, *Panesthia cribrata* Saussure and *Panesthia tryoni tryoni* Shaw (Blattodea: Blaberidae), and found a high degree of thelastomatoid sharing; seven of 13 species were shared. Here we compare the thelastomatoid fauna of *P. cribrata* and *P. tryoni tryoni* with that of (1) several other species of log-dwelling, wood-feeding arthropods and (2) several leaf-litter dwelling, detritus feeding arthropods all of which are from families known to be parasitized by thelastomatoids. The study explores the role of

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ecological niche overlap in the distribution of thelastomatoids across taxonomically diverse host groups.

## 2. Materials and methods

All arthropod specimens were collected from fallen logs and the forest floor within Lamington National Park, Queensland, Australia (28°12'S, 153°11'E) from 2002 to 2005. All panesthiine cockroaches were identified to species as per Roth [12]. All other arthropods were identified using voucher specimens lodged in the University of Queensland Insect Collection and as per CSIRO [13].

A transverse incision was made along the posterior end of the abdomen. The hindgut was then teased out into 0.85% saline and severed at the point just anterior to the origin of the Malpighian tubules. The excised hindgut was dissected and all nematodes found were extracted and preserved in fresh 70% ethanol.

Preserved nematodes were placed in a 5% solution of glycerol in 95% ethanol. These were left uncovered for 48 h to allow the ethanol to evaporate, thereby leaving the specimens in 100% glycerol. This was done to limit any damage to the worms caused by rapid transfer to pure glycerol. The nematodes were mounted in glycerol using the wax-ring method as described by Hunt [14]. All nematodes were identified using a morphological character database compiled from the literature as outlined in Jex et al. [11].

## 3. Results

### 3.1. Thelastomatoid host specificity from the literature

Examination of the literature shows that the five families that comprise the Thelastomatoidea have highly variable levels of host specificity (Tables 1 and 2).

### 3.2. Thelastomatoid host specificity from our experimental data

In total, 145 arthropod individuals were dissected: 53 *Panesthia cribrata*, 31 *P. tryoni tryoni*, 26 other log-dwelling arthropods and 35 leaf-litter dwelling arthropods (Table 3). Thirteen thelastomatoid species were found. Of these, twelve species belong to the Thelastomatidae: *Aoruioides queenslandensis* Jex, Schneider and Cribb, 2004, *Bilobostoma exerovulvae* Jex, Schneider, Rose and Cribb, 2006, *Blattophila praelongacoda* Jex, Schneider, Rose and Cribb, 2006, *Blattophila sphaerolaima* Cobb, 1920, *Cordonicola gibsoni* Jex,

Schneider, Rose and Cribb, 2006, *Coronostoma australiae* Jex, Schneider, Rose and Cribb, 2006, *Desmicola ornata* Jex, Schneider, Rose and Cribb, 2006, *Hammerschmidtella hochi* Jex, Schneider, Rose and Cribb, 2006, *Leidynemella fusiformis* Cobb in Chitwood and Chitwood, 1932, *Malaspinanema goateri* Jex, Schneider, Rose and Cribb, 2006, *Tsuganema cribratum* Jex, Schneider, Rose and Cribb, 2006 and one undescribed species, referred to herein as undescribed sp. 1. One species belonged to the Travassosinematidae: *Travassosinema jaidenae* Jex, Schneider, Rose and Cribb, 2006.

Of these thirteen species, seven were shared between the two panesthiine species and the other log-dwelling arthropods. *Blattophila sphaerolaima* was found in *P. cribrata*, *P. tryoni tryoni* and an unidentified millipede, Glomerid sp. 1 (Diplopoda: Glomeridae). *Blattophila praelongacoda* was found in *P. cribrata* and the passalid beetle, *Mastachilus quaestionis* (Kuwert). *Cordonicola gibsoni* was found in *P. cribrata*, *P. tryoni tryoni*, *M. quaestionis* and an unidentified millipede, Polydesmid sp. 1 (Diplopoda: Polydesmidae). *Leidynemella fusiformis* was found in *P. cribrata*, *P. tryoni tryoni* and *M. quaestionis*. *Aoruioides queenslandensis* was found in *P. cribrata*, *P. tryoni tryoni* and Glomerid sp. 1. *Travassosinema jaidenae* was found in *P. cribrata*, *P. tryoni tryoni*, and Polydesmid sp. 1. Undescribed sp. 1 was found in *P. tryoni tryoni*, *M. quaestionis* and Polydesmid sp. 1. The remaining six species were found only in the panesthiine cockroaches. No thelastomatoids were shared between the panesthiine cockroaches and any leaf-litter dwelling arthropods. No attempt was made to determine whether any of the nematodes not found in panesthiines were shared between other host groups.

## 4. Discussion

### 4.1. Inference of thelastomatoid host specificity from the literature

All 89 species of hystriagnathids, comprising 21 genera, and consisting of 113 host–parasite–locality combinations (HPLCs) are found exclusively in passalid beetles (Coleoptera: Passalidae). Additionally, all 26 species of pseudonymids, comprising five genera, and consisting of 36 HPLCs, are found exclusively in water beetles (Coleoptera: Hydrophilidae). With the exception of *Protrellata alii* from *Gryllus domesticus* (Orthoptera) from India [15], all 22 species of protrelloidids, consisting of four genera, and 26 HPLCs, are found in cockroaches (Blattodea). With the exception *Travassosinema* spp., which have been reported from five diplopod species and one

Table 1  
Host specificity at the familial level for the Thelastomatoidea based on the records from the literature

Parasite family	Blattodea	Coleoptera	Diplopoda	Diptera	Oligochaeta	Orthoptera	Arachnida
Hystriagnathidae		113					
Protrelloididae	26					1	
Pseudonymidae		36					
Thelastomatidae	137	38	80	21	1	16	1
Travassosinematidae	2		5			46	

Numbers represent host–parasite–locality combinations.

Table 2  
Thelastomatoid genera infecting multiple host orders, based on records from the literature

Parasite genus	Blattodea	Coleoptera	Diplopoda	Diptera	Oligochaeta	Orthoptera	Arachnida
<i>Thelastomatidae</i>							
<i>Aorurus</i>		1	4				
<i>Blatticola</i>	18		1				
<i>Cephalobellus</i>	3	17	22	20			
<i>Coronostoma</i>	1	1	6				
<i>Corydiella</i>	1	1					
<i>Desmicola</i>	1	1	3				
<i>Euryconema</i>	1					1	
<i>Hammerschmidtella</i>	24		3				
<i>Johnstonia</i>		2	5				
<i>Leidynemella</i>	4		1				
<i>Robertia</i>		1	1				
<i>Severianoia</i>	3		1				
<i>Tetleyus</i>		2	1	1			
<i>Thelastoma</i>	22	12	29		1		1
Total	78	38	77	21	1	1	1
<i>Travassosinematidae</i>							
<i>Travassosinema</i>	1		5				
Total	1		5				

Numbers represent host–parasite–locality combinations.

blattodean, and 1 *Binema* spp., reported from a diplopod, all 20 travassosinematid species, comprising 9 genera and 46 HPLCs are found exclusively in mole crickets (Orthoptera: Gryllotalpidae). All of these families of thelastomatoids appear to be highly host specific.

Only the type family, Thelastomatidae, shows an appreciably low level of host specificity at the familial level. Of the 195 described species, in 41 genera, and consisting of 294 HPLCs, 77 species parasitize blattodeans, 58 species parasitize diplopods, 34 species parasitize coleopterans, 11 species parasitize orthopterans, four species parasitize dipterans, one species, *Thelastoma pterogon*, parasitizes an oligochaete worm, and one, *Thelastoma euscorpia*, parasitizes a scorpion (Arachnida). Thus, the Thelastomatidae would appear to have low host specificity.

However, interpretation of host specificity based solely upon reports from the literature is highly susceptible to

inaccuracies as a result of incomplete reportings, nominal species, inaccurate records and incorrect host or parasite taxonomic hypotheses. It is probable that the records for the Thelastomatoidea are sufficiently complete to accept that there are high levels of host specificity, at least at the familial level, within the hystrignathids, pseudonymids and protrelloidids. The record also suggests that there is, if not high specificity, at least a predisposition within the travassosinematids for gryllotalpid hosts. Importantly, all four of these families have been judged to be monophyletic based on various morphological characters [1]. In contrast, the record would suggest that thelastomatids have very low specificity. However, no justification for monophyly has been found for this group [1]. Although this does not preclude the possibility that the family is indeed monophyletic it does raise the possibility that the apparent low specificity is the result of a paraphyletic host lineage.

Table 3  
Thelastomatoid fauna of *Panesthia cribrata* and *Panesthia tryoni tryoni* and other ecologically similar and disparate arthropods at Lamington National Park

Host species	Habitat	n	Aq	Be	Bp	Bs	Ca	Cg	Do	Hh	Lf	Mg	U1	Tc	Tj
<i>P. cribrata</i>	Fallen logs	53	37	1	1	9		43		3	1	2		22	4
<i>P. tryoni tryoni</i>	Fallen logs	31	21	3		6	3	30	6		11	4	1	16	9
<i>M. quaectionis</i>	Fallen logs	14			2			1			7		3		
Polydesmid sp. 1	Fallen logs	8						1					1		2
Glomerid sp. 1	Fallen logs	1	1			1									
Polydesmid sp. 2	Fallen logs	3													
<i>Methana</i> sp.	Leaf-litter	18													
Blattid sp. 1	Leaf-litter	6													
<i>Australostygygyga</i> sp.	Leaf-litter	8													
Blattid sp. 1	Leaf-litter	2													
<i>Loxta</i> sp.	Leaf-litter	1													

Aq = *Aoruroides queenslandensis*; Be = *Bilobostoma exorovulvae*; Bp = *Blattophila praelongacoda*; Bs = *Blattophila sphaerolaima*; Ca = *Coronostoma australiae*; Cg = *Cordonicola gibsoni*; Do = *Desmicola ornata*; Hh = *Hammerschmidtella hochi*; Lf = *Leidynemella fusiformis*; Mg = *Malaspinanema goateri*; U1 = undescribed sp. 1; Tc = *Tsuganema cribratum*; Tj = *Travassosinema jaidenae* (n=number of specimens dissected).

The thelastomatids appear to be more host specific at the generic level than at the familial level, with 27 of the 41 recognized thelastomatid genera parasitizing single host orders. However, analyzing specificity at the genus level is complicated by the fact that few genera are large enough to allow the elucidation of real patterns. Within the Thelastomatidae, we judge seven genera to be large enough to allow for reliable interpretation of their host specificity: *Blatticola* (11 species), *Blattophila* (11 species), *Cephalobellus* (28 species), *Hammerschmidtella* (11 species), *Johnstonia* (7 species), *Leidynema* (7 species) and *Thelastoma* (51 species). All species of *Blatticola* are found in cockroaches, except *B. caucasica* which is found in a millipede [16]. *Blattophila* spp. are all found in cockroaches. Two species of *Hammerschmidtella* are found in millipedes; the other nine species are found in cockroaches. Two species of *Johnstonia* are found in beetles; the remaining five species are found in millipedes. All species of *Leidynema* are found in cockroaches. The host ranges for *Cephalobellus* and *Thelastoma* are much more variable. Sixteen of the 28 described *Cephalobellus* spp. (57.1%) are found in beetles, seven species (25.0%) found in millipedes, three species (10.7%) found in flies and three species (10.7%) found in cockroaches (one species, *Cephalobellus galliardi*, is recorded for a beetle and a millipede). *Thelastoma* is by far the largest thelastomatoid genus. It also has the most diverse host range. Twenty-five of the 51 described *Thelastoma* spp. (49.0%) are from millipedes, 15 species (29.4%) are from cockroaches, nine species (17.6%) are from beetles, one species (0.2%) has been described from a scorpion, and one species (0.2%) has been described from an oligochaete worm.

The vast majority of thelastomatoid species (274 of 348; 78.7%) have been described from a single host species (Fig. 1A). This suggests that infection of multiple host species is not a common trait within this superfamily; however, there are few thelastomatoid species for which there are multiple records suggesting the group is not well known (Fig. 1B). Only five thelastomatoid species have been reported to parasitize more than one host order. *Aorurus agile* (Leidy, 1949), *Cephalobellus galliardi* (Dollfus, 1952) and *Coronostoma diplopodicola* (Dollfus, 1964) each parasitize two millipede and one beetle species [17–25]. *Binema mirzaia* (Basir, 1940) parasitizes one cockroach and one mole cricket species. Lastly, *Desmicola moramangi* (Van Waerebeke, 1969) parasitizes one beetle and one millipede species [24]. As with the thelastomatoid record at the family level, judgments of host specificity at the species level for the Thelastomatoidea based upon the literature are highly problematic. Foremost among these difficulties are nominal species descriptions, incorrect reportings and incomplete records. An unfortunate dilemma within the Thelastomatoidea is that the group is in woeful need of a comprehensive monographic study. The last major review was undertaken over a decade ago [8–10] and although this study provided a thorough cataloguing of the species within the group and proposed a number of synonymies, it is not a monographic study and, presumably, was not intended to be, providing no redescrptions of old taxa and no taxonomic key for the group. As a result, many of the species currently recognized within the Thelastomatoidea

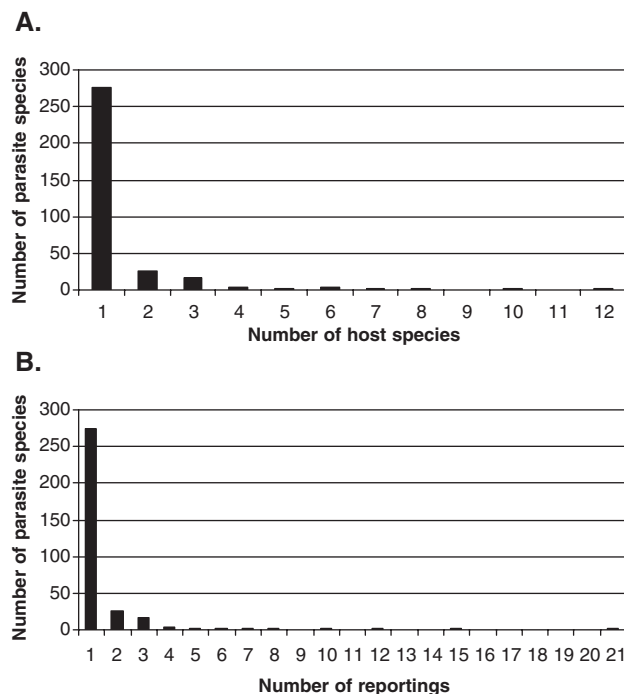


Fig. 1. Frequency of multiple hosts and multiple reportings for Thelastomatoidea from the literature. A. Number of hosts per thelastomatoid species. B. Number of reportings per thelastomatoid species.

have been derived from outdated descriptions that are not sufficient for confident reidentification and numerous species within the superfamily are candidates for redesignation as *species inquirenda*. This presents a significant difficulty when assessing levels of specificity within the superfamily. Species that are inadequately described and cannot be confidently reidentified obscure these relationships and result in a number of “dead-end” entries that appear to be highly specific but are, in fact, artifacts. This difficulty is perhaps overshadowed by the vastly incomplete host record. As demonstrated in Fig. 1B, the enormous majority (78.7%) of thelastomatoid species are only known from single recordings, having been found once, described and never presented or recorded again. We contend that the apparent high specificity suggested by the records in the literature for thelastomatoid species is an artifact of an immensely incomplete host record with the vast majority of species having yet to be described. There are approximately 350 described thelastomatoid species, however, considering the massive diversity of its host group, the Arthropoda, it seems entirely possible that the true richness for the superfamily is one or more orders of magnitude larger than this total. Until the record for the Thelastomatoidea is much more complete, judgments based on the literature for species level specificity are highly suspect and arbitrary. As such, the only reliable way to determine specificity within the group is through direct examination.

#### 4.2. Thelastomatoid host specificity from experimental data (Table 3)

Upon examination of host specificity in parasitic nematodes, Inglis [26] suggested that host specificity was likely the result of

two mechanisms: host physiology, such as its immune system and tissue type; and host ecology, such as food source or habitat. He suggested that in the case of pinworms, the latter was the most likely cause of specificity. Our findings are consistent with Inglis's [26] hypothesis that host-specificity within the Oxyurida is largely dictated by host ecology.

In total, seven of the 13 (54%) thelastomatoid species reported from *P. cribrata* and *P. tryoni tryoni* were shared with other log-dwelling arthropods. All non-panesthiine log-dwelling arthropods, except *Polydesmid* sp. 2, shared at least one thelastomatoid species with either *P. cribrata* or *P. tryoni tryoni*. In total, of the 26 non-panesthiine log-dwelling arthropods examined there were 19 instances of sharing. In contrast, none of thirty-five leaf-litter dwelling arthropods showed any thelastomatoid faunal overlap with log-dwelling species.

Thus, we find a high degree of thelastomatoid species sharing between panesthiines and other log-dwelling, wood-feeding arthropods and no sharing of thelastomatoid species between panesthiines and leaf-litter dwelling arthropods. Considering that thelastomatoids are transmitted directly by infective eggs, this is to be expected. Leaf-litter dwelling cockroaches, such as *Methana* sp. and *Loxta* sp., are not likely to have a significant level of niche overlap with log-dwelling arthropods, such as *P. cribrata* and *P. tryoni tryoni*. Considering that they feed on decaying leaves (versus decaying wood) and live in different habitats (forest floor versus fallen logs), the opportunity for cross-infection of thelastomatoids are unlikely to be met. In contrast, the taxa with which thelastomatoids of the panesthiines are shared live in essentially exactly the same habitat as the panesthiines and appear to ingest much the same food such that there is presumably continual exposure to cross-infection.

This study provides direct experimental evidence that thelastomatoids are shared across host orders. Examinations of the thelastomatoid reports from the literature suggest this is rare. Only five of the approximately 350 described species have been previously reported from multiple orders. However, the vast majority of thelastomatoid species are described from single host-locality reports. We suspect that the level of specificity apparent from examination of host reportings is misleading, and probably a reflection of our limited knowledge of this group rather than a true indication of the real levels specificity. We predict that many thelastomatoid species presently reported from single host species will be found to infect numerous host groups if other arthropods sharing the same spatial and ecological niches as their known hosts are examined.

Ecological niche overlap appears to be extremely important in determining the boundaries of the host range for thelastomatoid species. In this study we found a high degree of sharing between ecologically similar arthropods, and no sharing between ecologically disparate ones. This may also reflect upon the level of specificity inferred from the literature, particularly for the Pseudonymidae. Pseudonymids have been reported only from water beetles (Coleoptera: Hydrophilidae). Given the large division in ecological niche between aquatic

and terrestrial arthropods, the apparent specificity of this family may be a reflection of its host ecology rather than parasite specificity. Further direct examinations of hosts and their thelastomatoid parasites are necessary to accurately demonstrate the levels of host specificity within this superfamily.

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## References

- [1] Adamson ML. Evolutionary biology of the Oxyurida (Nematoda): biofacies of a haplodiploid taxon. *Adv Parasitol* 1989;28:175–228.
- [2] Brooks DR, Glen DR. Pinworms and primates: a case study in coevolution. *Proc Helminthol Soc Wash* 1982;49:76–85.
- [3] Hugot JP, Gardner SL, Morand S. The Enterobiinae subfam. nov. (Nematoda, Oxyurida) pinworm parasites of primates and rodents. *Int J Parasitol* 1996;26(2):147–59.
- [4] Hugot JP. Phylogeny of neotropical monkeys: the interplay of morphological, molecular, and parasitological data. *Mol Phylogenet Evol* 1998;9:408–13.
- [5] Adamson ML, Nasher AK. Pharyngodonids (Oxyuroidea: Nematoda) of *Agama adramitana* in Saudi Arabia with notes on *Parapharyngodon*. *Can J Zool* 1984;62:2600–9.
- [6] Adamson ML, Nasher AK. Pharyngodonidae (Oxyuroidea: Nematoda) of *Agama yemenensis* in Saudi Arabia: hypothesis on the origin of pharyngodonids of herbivorous hosts. *Syst Zool* 1985;6:299–318.
- [7] Adamson ML. Evolutionary patterns in life histories of Oxyurida. *Int J Parasitol* 1994;24:1167–77.
- [8] Adamson ML, van Waerebeke D. Revision of the Thelastomatoidea, Oxyurida of invertebrate hosts: 1. Thelastomatidae. *Syst Parasitol* 1992;21:21–64.
- [9] Adamson ML, van Waerebeke D. Revision of the Thelastomatoidea, Oxyurida of invertebrate hosts: 2. Travassosinemitidae, Protrelloididae and Pseudonymidae. *Syst Parasitol* 1992;21:169–88.
- [10] Adamson ML, van Waerebeke D. Revision of the Thelastomatoidea, Oxyurida of invertebrate hosts: 3. Hystrignathidae. *Syst Parasitol* 1992;22:111–30.
- [11] Jex AR, Schneider MA, Rose HA, Cribb TH. The Thelastomatoidea (Nematoda: Oxyurida) of two sympatric Panesthiinae (Blattodea) from south-eastern Queensland, Australia: taxonomy, species richness and host specificity. *Nematol* 2006;7:543–75.
- [12] Roth LM. A taxonomic revision of the Panesthiinae of the world: I. The Panesthiinae of Australia (Dictyoptera: Blattodea: Blaberidae). *Aust J Zool* 1977 [Supplementary Series No. 48:1–112].
- [13] CSIRO. The Insects of Australia. A textbook for students and research workers. Carlton: Melbourne University Press; 1991.
- [14] Hunt DJ. The African Rhigonematoidea (Nematoda: Rhigonematida): 2. Six new species of *Rhigonema* Cobb, 1989 (Rhigonematidae). *Nematol* 2002;4:803–27.
- [15] Farooqui MN. Some known and new genera and species of the family Thelastomatidae Travassos, 1929. *Riv Parassitol* 1970;31:195–214.
- [16] Skrzabin KI. Sur deux nouveaux nematodes parasites de myriapodes. *Annu Mus Zool Acad Sci URSS, Leningrad* 1927;27:304–9.
- [17] Wright K. Trichomycetes and oxyuroid nematodes in the millipede *Narceus annularis*. *Proc Acad Nat Sci Phil* 1979;76:49–163.

- [18] Leidy J. New genera and species of Entozoa. *Proc Natl Acad Sci* 1849;4:225–33.
- [19] Christie JR. Some nematode parasites (Oxyuridae) from coleopterous larvae. *J Agric Res* 1931;42:463–82.
- [20] Kloss GR. Parasitos intestinaux do diplopoda *Scaphiostreptus buffalus* Schubart. *Bol Mus Para Emílio Goeldi Zool* 1961;35:11–3.
- [21] Dollfus R. Quelques Oxyuroidea de myriapodes. *Ann Parasitol Hum Comp* 1952;27:143–236.
- [22] Jarry DT. Les Oxyurides de quelques arthropodes dans le midi de la France. *Ann Parasitol Hum Comp* 1964;39:381–508.
- [23] Theodorides J. Contribution à l'étude des parasites et phoretiques de coleopteres terrestres. *Vie Milieu Ser C Biol* 1955;310 [Supplement 4].
- [24] van Waerebeke D. Quelques nematodes parasites de blattes à Madagascar. *Ann Parasitol Hum Comp* 1969;44:761–76.
- [25] Dollfus R. Nematodes de myriapodes du Congo Belge 1re contribution. *Mem Mus Nat Hist Nat Nouv Ser A* 1964;32:109–69.
- [26] Inglis WG. Speciation in parasitic nematodes. *Adv Parasitol* 1971; 9:185–223.