A review of the endoparasites of the lemurs of Madagascar

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Abstract

The lemurs of Madagascar have received intense research attention in recent years and decades, as researchers attempt to discern the extent of their ecological adaptations and phylogenetic diversity. In contrast, the natural history of lemur parasites is currently poorly understood and understudied. After a brief period of great progress in naming and describing lemur parasites in the 1950s and 1960s, few researchers have studied lemur parasites, and recent studies tend to be more ecologically oriented (e.g. considering impact on the host species) rather than basic studies geared towards understanding parasite diversity. In this paper, we review the current state of knowledge of lemur parasites, including Nematoda (roundworms), Platyhelminthes (flatworms), Acanthocephala (thorny-headed worms), and Protozoa. There have been 27 helminth species and 12 protozoan species described from lemurs (excluding infections likely acquired in captivity, species which have since been synonymized, and misclassifications). These species likely represent only a fraction of the existing diversity; research efforts devoted to describing and classifying species have been brief, largely focused on helminths (especially nematodes), and restricted to a small number of reasonably accessible sites and host species. Given the important effects that parasites can have on host abundance, behavior and social systems (and the fact that many lemur species are threatened with extinction), it is important to increase our understanding of their naturally-existing diversity. This knowledge will not only help fill in the gaps of our understanding of Malagasy natural history, but will also be important baseline data for lemur population monitoring.

Résumé détaillé

Les lémuriens de Madagascar ont été bien étudiés dans les années et décennies récentes, car les chercheurs tentent de discerner l'étendue de leurs adaptations écologiques et de leur diversité phylogénétique. Toutefois, notre connaissance de l'histoire naturelle des parasites de lémuriens reste vraiment incomplète. Il y a eu une période brève de grand progrès, dans les années 1950 et 1960, durant laquelle les chercheurs ont nommé et décrit beaucoup d'espèces de parasites de lémuriens; ces travaux étaient menés surtout par quelques chercheurs français pré- et post-indépendance. Cependant, après cette période, très peu d'études ont été entreprises pour continuer cette tradition. Les études récentes, par ailleurs, sont surtout axées sur l'écologie (par exemple en considérant l'impact du parasite sur l'espèce-hôte).

Dans cet article, nous réexaminons l'état actuel des connaissances sur les parasites de lémuriens : Nematoda (vers ronds), Platyhelminthes (vers plats), Acanthocephala (vers à tête épineuse), et protozoaires. Vingt sept espèces d'helminthes (22 Nematoda, trois Platyhelminthes et deux Acanthocephala) et 12 espèces de protozoaires ont été décrites chez les lémuriens (sans compter les infections acquises probablement en captivité, les espèces qui ont été synonymizées, et les erreurs d'identification). Pour ces espèces, nous donnons un sommaire de la taxonomie, la morphologie, les circonstances de leur découverte, et les récoltes connues à travers les espèces de lémurien et les sites. Nous fournissons aussi un tableau avec les caractéristiques morphologiques des oeufs des parasites de lémuriens trouvés dans les échantillons fécaux. Les espèces de parasites connues aujourd'hui représentent probablement une partie seulement de la diversité existante, pour plusieurs raisons. Premièrement, les efforts de recherche consacrés à décrire et classer les espèces ont été brefs, principalement limités aux années 1950 - 1960, et à un petit nombre de sites et aux espèces les plus accessibles. Deuxièmement, ces études

ont été principalement centrées sur les helminthes (surtout les nématodes) et ont eu tendance à négliger d'autres groupes, surtout les protozoaires. La diversité parasitaire plus faible que pour les autres familles de primates signifie vraisemblablement que des espèces restent encore à découvrir.

Il est important d'augmenter notre compréhension de la diversité naturelle existant chez les parasites de lémuriens (et autre faune) à Madagascar, premièrement pour combler nos lacunes en histoire naturelle, mais aussi parce que les recherches récentes révèlent les effets importants que les parasites peuvent avoir sur l'abondance des hôtes, leur comportement et leur organisation sociale. Dans le contexte des études des lémuriens, notre connaissance des parasites des lémuriens reste relativement faible (également leur diversité et leur écologie); les parasites sont les paramètres moins visibles que d'autres tels que l'agression, l'affiliation, la sélection sexuelle et les choix comportementaux lors de la réproduction. Il en résulte que les biologistes étudiant les lémuriens manquent une partie important du cadre écologique pour comprendre leur biologie, leur comportement et leur organisation sociale.

La façon la plus accessible et la moins intrusive pour étudier des parasites chez les lémuriens sauvages est d'observer les oeufs dans les fèces, et c'est la méthode utilisée dans la plupart des études des 20 années passées. Cependant, la connaissance qui en résulte est limitée parce que les déterminations fondées sur les oeufs ne dépassent pas le niveau du genre ou de la famille, alors que les adaptations des parasites et des effets sur l'hôte peuvent varier même entre des espèces très proches. En raison des restrictions éthiques qui empêchent les chercheurs de tuer les lémuriens pour recueillir leurs parasites, il est beaucoup plus difficile maintenant de collecter des échantillons adultes de parasites de lémuriens (surtout des helminthes) que dans les années 1950 et 1960. Cependant, les chercheurs peuvent encore étudier la diversité spécifique, en disséquant les animaux morts accidentellement et en cultivant les larves des oeufs trouvés dans les fèces.

Les connaissances obtenues sur les sites de recherche des lémuriens à Madagascar seraient des données vraiment importantes pour le suivi écologique. Elles peuvent nous aider à étudier les futurs changements dans la distribution et l'abondance des parasites (par exemple, pour comprendre les impacts des pressions anthropiques), et à comprendre, potentiellement, les effets complexes sur l'écologie de population et le comportement de l'hôte. Ceci est surtout important pour les espèces de lémuriens car elles sont menacées d'extinction, maintenant ou dans le futur.

Introduction

The lemurs of Madagascar are a unique and endemic primate radiation, thought to have resulted from the arrival of a single common ancestor to the island approximately 50-60 million years ago (Yoder, 1996; Poux *et al.*, 2005; Mittermeier *et al.*, 2006). The past 25 years have seen concerted and increasing efforts to identify and catalogue the sometimes-cryptic diversity in lemur species (Mittermeier *et al.*, 2006; Tattersall, 2007); currently the extant portion of the radiation contains 71 recognized taxa (68 species with a total of 71 subspecies), with an additional 16 species known only from subfossil remains. In contrast, little attention is being paid to cataloguing or otherwise studying their endoparasites. Early authors noted that helminth parasites of lemurs were seriously understudied relative to those of primates on other continents (Chabaud & Petter, 1958). Much progress has been made since then but the field today remains rather dormant, and there are relatively few helminth parasites known from wild lemurs relative to other taxa (Figure 1). Among Old World primates, the great apes (Hominidae) and Old World monkeys (Cercopithecidae) have had many more helminth parasites described than lemurs (5 families), galagos (Galagonidae), lorises (Lorisidae), and lesser apes (Hylobatidae). This discrepancy is likely a difference in the intensity of research rather than a reflection of differences in true species richness.

The intensity of the study of helminth parasites of lemurs has varied drastically over time. There were apparently no studies before the French colonization in 1896 except the single mention of *Trichuris lemuris* by Rudolphi in 1819, and very few in the first few decades of French rule (up until the 1940's; largely because the lemurs themselves were understudied during this time). In the 1950's and 1960's the study of lemurs in their natural habitat intensified, sponsored by l'Office de la Recherche Scientifique et Technique Outre-Mer, ORSTOM) and carried out almost single-handedly by Jean-Jacques Petter and Arlette Petter-Rousseaux of the Muséum national d'Histoire naturelle in Paris. Seemingly as a byproduct of these advances, the study of lemur parasites also intensified in the same period, led by Alain Chabaud, Edouard Brygoo, and Annie Petter.

Following Malagasy independence in 1960, the country experienced a continuation of biological
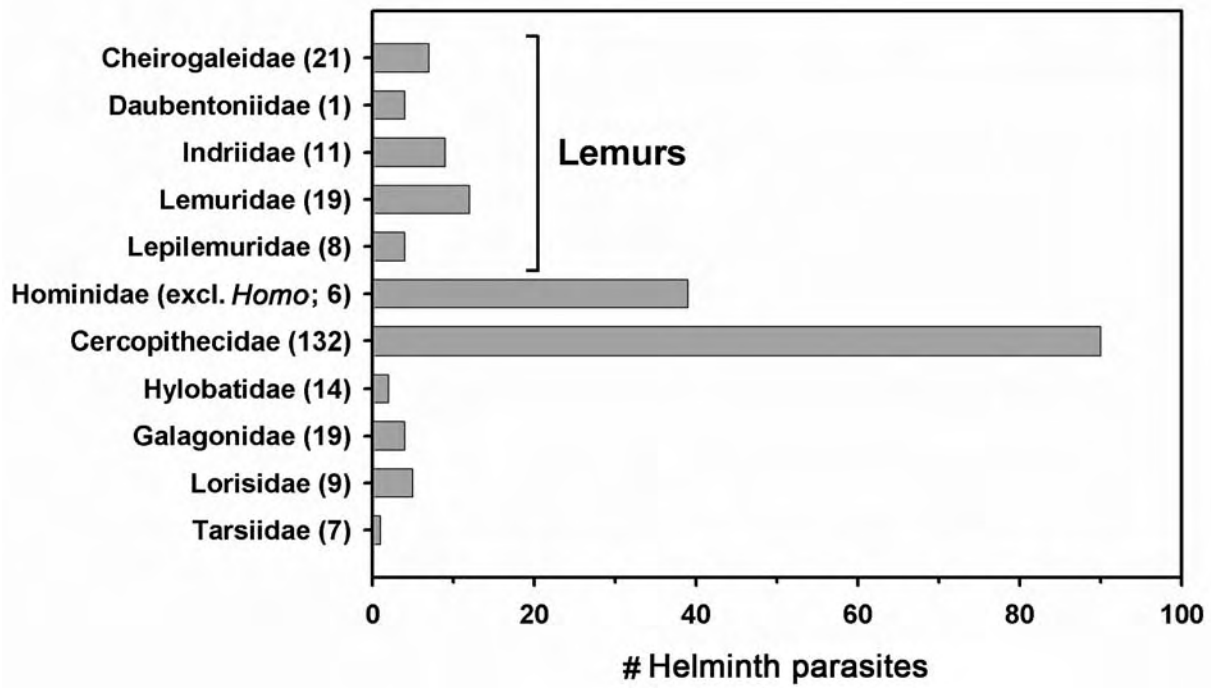
Figure 1. Minimum number of helminth parasite species documented in Old World primate families (number of species per family in parentheses). Parasite data from Global Mammal Parasite Database, www.mammalparasites.org (Nunn & Altizer, 2005); primate taxonomy following Wilson & Reeder (2005).
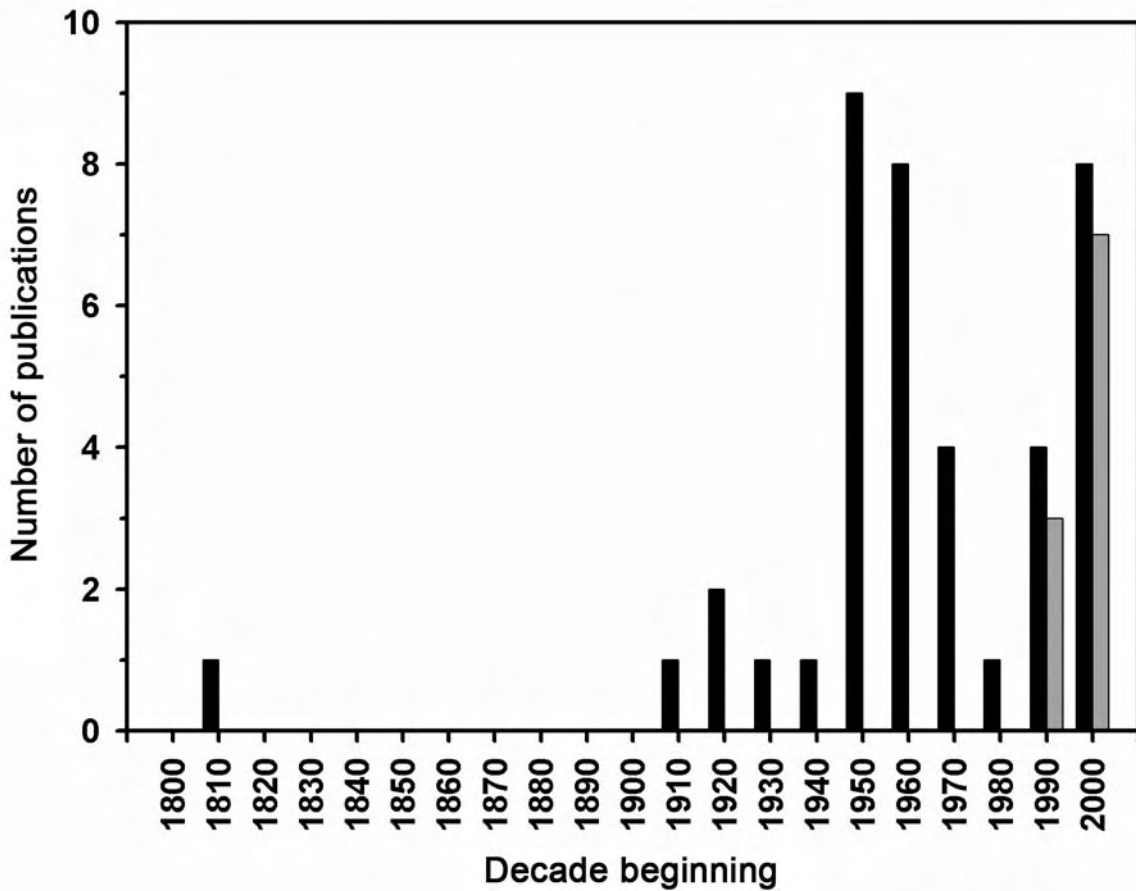

Figure 2. Temporal distribution of publications (journal articles, book chapters, and postgraduate theses; n=57) relating to ecto- and endoparasites of lemurs in the wild. Black bars denote publications primarily devoted to parasites, grey bars denote publications with other principal foci (e.g. health assessments, evolution, etc.).

research by scientists from France and other countries, including more pioneering studies of lemurs, but parasitological work waned compared to the 1950s and 1960s. Then, with the coming of the "second republic" and new President Didier Ratsiraka in 1975, scientific research reduced dramatically as Madagascar largely closed its doors to outside research.   In the mid-1980s wider government reforms and the development of the country's first Environmental Action Plan helped biological research be re-started, but the study of parasitology has not re-attained the level of activity it achieved in the 1960s.

The temporal distribution of published studies reflects this history (Figure 2): a single mention by Rudolphi in 1819, a few studies in the early colonial years (1910s-1940s), a peak in the 1950s and 1960s, a waning in the 1970s and 1980s, and a rebound in the 1990s and 2000s. However, the rebound in the 1990s and 2000s consist of largely different kinds of parasitological studies. First, the proportion of studies for which parasitology is just one part of a larger study (e.g. health assessments, immunology) is much higher (Figure 2). Second, the temporal distribution of studies, which name new helminth parasites of lemurs, shows the same trends except there is no rebound in the 1990s and 2000s (Figure 3). This is because many of the studies in the 1950s and 1960s are descriptions of adult worms from necropsy, either of animals that died in captivity or in some cases animals hunted and killed (with authorization from the French colonial government) for the sole purpose of describing their parasites (Chabaud *et al.*, 1961a).

New ethical restrictions prevent the capture of wild primates for similar purposes today, but even opportunistic necropsies of animals dying of natural causes or fecal cultures have not been employed to describe adult parasites. Instead, most recent studies have focused on non-invasive sampling of feces, with descriptions and counts of helminth eggs. As a result, extremely little progress has been made in the past three decades in terms of documenting the diversity of lemur endoparasites; indeed 20 of the 27 described helminth parasites were described in the 1950s and 1960s, with 26 of the 27 already known by 1972. Such new research directions may yield important information about parasite ecology, seasonality, and transmission, but these data are hard to interpret without a taxonomic context. For example documenting "strongyle" eggs in several sympatric species might indicate a single helminth species with free interspecific transmission or several strongyle species with morphologically similar eggs. Without

a better understanding of the diversity of strongyle parasites in Madagascar (only one, *Lemurostrongylus residuus* has been described), such data are difficult if not impossible to interpret.

This paper summarizes the current knowledge of endoparasites infecting wild lemurs, and reviews their taxonomy, morphology, host species, and tools for diagnosis. The species reviewed include gastrointestinal helminths, helminths occupying other body tissues (e.g. filaria), gastrointestinal Protozoa, and Protozoa infecting the blood (e.g. malaria). We exclude species described in captive lemurs unless there is strong indication that the parasite is present in wild populations. Descriptions include both the adult anatomy (for identification to species level) and the anatomy of eggs (to identify as precisely as possible eggs found in fecal samples). Taxonomy follows Anderson (2000) and Salgado-Maldonado (2005). This paper is the first review of lemur endoparasites in over 40 years, since that of nematodes by Chabaud *et al.* (1965).

1. Nematoda
Order Strongylida
Superfamily Strongyloidea
Family Chabertiidae
Lemurostrongylus
Lemurostrongylus residuus Chabaud, Brygoo & Petter, 1961

History – Chabaud *et al.* (1961a) described *Lemurostrongylus residuus* from approximately 100 worms recovered from the posterior third of the intestine of a *Hapalemur griseus* killed at Périnet (=Analamazaotra) in 1961. In the 46 years that have passed since the original description, no authors have documented adults of this species or a congener from any other lemur species.

Morphology – Females ~ 9.0 mm long, maximum width 310 μm, with short tail (90 μm) narrowed directly behind the anus. Vulva located 150 μm anterior to anus, ovejector composed of the three sections typical of Strongylida; eggs measure 62 x 38 μm. Males ~ 7.8 mm long, maximum width 240 μm, with a large caudal bursa (265 μm wide x 175 μm tall) and two simple, long (675 μm) spicules.

Cylindrical body, thick cuticle with transverse striae of ~ 6.5 μm spacing. Cephalic extremity separated from rest of body by a constriction just behind the buccal cavity (~ 35 μm from the apex). Head flat, with four large submedian papilla and two large, flat amphids. Mouth circular, with a prominent ring composed of 6,
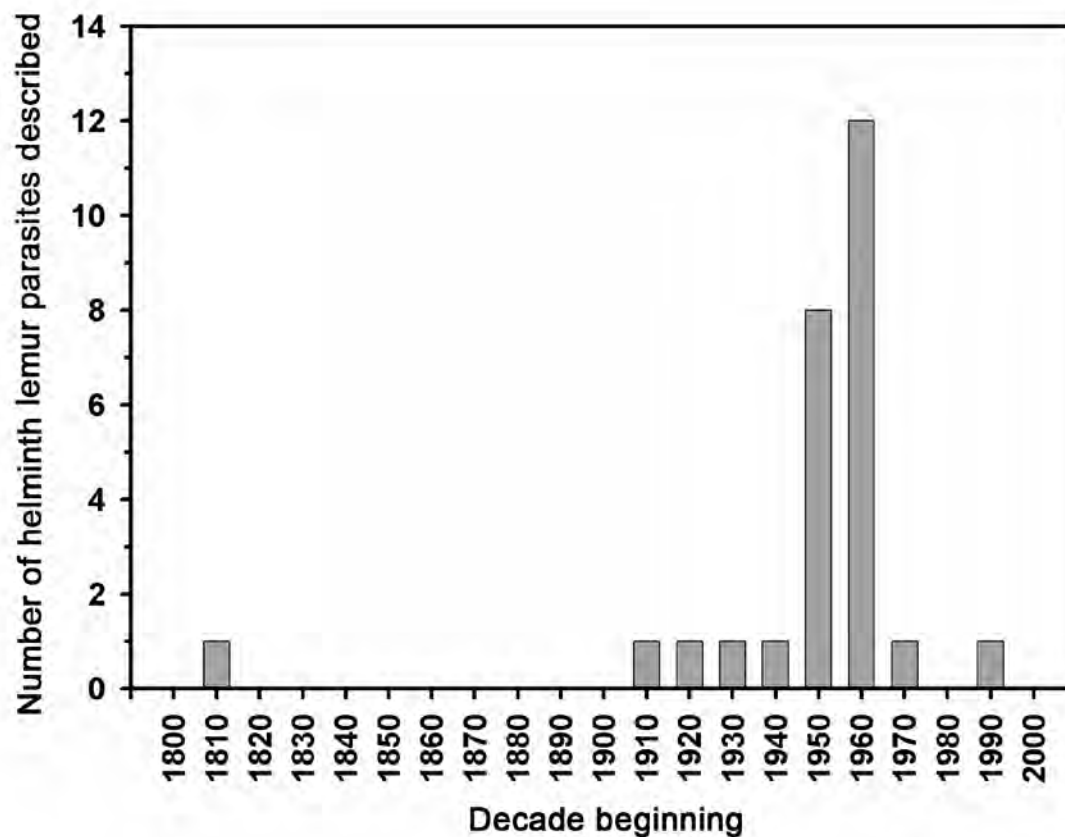
Figure 3. Temporal distribution of original descriptions of the 27 recognized helminth parasites of Malagasy lemurs in the wild (Rudolphi, 1819; Beddard, 1911; Chandler, 1929; Baer, 1935; Kreis, 1945; Machado Filho, 1950; Chabaud & Choquet, 1955; Chabaud & Brygoo, 1956; Chabaud & Petter, 1958, 1959; Deblock & Capron, 1959; Chabaud *et al.*, 1961a, 1961b, 1964, 1965; Richard, 1965; Petter *et al.*, 1972; Hugot *et al.*, 1995).

8, or 10 segments. Thin-walled buccal capsule (35 μm wide x 15 μm tall), almost circular in transverse section.   Complex claviform esophagus including (from front to back): (1) a short pharyngeal portion, (2) a cylindrical corpus with "feathery" appearance well documented in *Murshidia*, (3) a distinct narrowing, and (4) a bulb becoming progressively larger towards the posterior end. Nerve ring at the anterior end of the narrowing, excretory pore at the posterior end. Two anteriorly pointed deirids found laterally just behind excretory pore.

Life cycle & mode of transmission – Unstudied. In related species (*Chabertia* spp., *Ternidens* spp., *Oesophagostomum* spp.) eggs are passed in the fecal stream, hatch and develop into ensheathed third-stage larvae during several days in the environment, with infection occurring through ingestion of third-stage larvae (Anderson, 2000).

Diagnosis at necropsy – Chabaud *et al.* (1961a) give little indication of the appearance or location of *Lemurostrongylus residuus* worms at necropsy except that they were located in the posterior third of the intestine.

Diagnosis in fecal examination – Based on closely related species one would expect a fecal-oral direct transmission with mature or maturing eggs found in feces.

Hosts – Adult worms only known from a single *Hapalemur griseus* individual killed at Périnet (=Analamazaotra) and described by Chabaud *et al.* (1961a).

Typical "strongylid" eggs have been found in fecal examinations of several species and provisionally identified as *Lemurostrongylus* sp.: *Eulemur fulvus albifrons* (Junge & Sauther, 2006), *Propithecus deckeni deckeni* (Junge & Louis, 2005), *Lepilemur edwardsi* (Junge & Sauther, 2006), *Varecia rubra* (Dutton *et al.*, in press), *Lemur catta* (Loudon *et al.*, 2006), *Indri indri*, *Hapalemur* spp., and *Varecia variegata* (Faulkner *et al.*, 2004), and *Propithecus diadema* (Irwin, unpub. data; Figure 4).   Other authors have identified typical "strongylid" eggs in fecal examinations but referred these to other genera: *Cheirogaleus medius* and *Microcebus murinus* (Raharivololona, 2006), *P. edwardsi*, *E. rubriventer*, *V. variegata*, *Prolemur simus*, *H. aureus*, *H. griseus*, and *Lepilemur* sp. (Hogg, 2002, in prep.).

Because strongylid eggs are generally indistinguishable based on gross morphology, the conservative position would be to regard all "strongyle" eggs found in lemur feces as *Lemurostrongylus* until proven otherwise. That said, additional strongyle diversity almost certainly remains undiscovered within wild lemur populations. This may include both additional species of *Lemurostrongylus*, which may prove to be specific to host species or genera (Hugot, 1999), or other genera (either known from other continents or as-yet undescribed).

Clinical signs – None recorded.

Order Strongylida
Superfamily Trichostrongyloidea
Family Trichostrongylidae
Subfamily Libyostrongylinae
Pararhabdonema
Pararhabdonema longistriata Kreis, 1945

History – Kreis (1945) described female *Pararhabdonema longistriata* worms from an *Avahi laniger* specimen of unknown provenience within Madagascar, acquired in 1931. Subsequently, Chabaud & Choquet (1955) described numerous adult specimens recovered from the "stomachs" of two *Lepilemur ruficaudatus* that died in Paris after one month in captivity. This second report described the morphology of both sexes. Finally, Chabaud *et al.* (1961a) described *P. longistriata* found in necropsy of *Indri indri* but provided no additional morphological description.

Morphology – Kreis (1945) described females measuring 40.5 - 43.4 mm long, maximum width 357-399 µm. Eggs are larvated and measure 66 (range 51.5-77.5) x 38 (range 34.5-43) µm. Chabaud & Choquet (1955) described smaller females measuring 25 mm long, with a width of 260 µm in the vulval region (20 mm from the anterior extremity), and a tail length of 240 µm. The genital apparatus is didelphic, with paired uteri (each 2 mm long) opening into a shared pars ejectrix; eggs are embryonated, ovoid and measure 70 x 42 µm. Males measure 16 mm and 140 µm in width and have well-developed caudal bursae and paired spicules (260 µm long).

Cylindrical body, thick cuticle with longitudinal ridges, which are interrupted at the level of each transverse stria. Cephalic extremity flattened, with 10 papilla and 2 amphids. Mouth has a rounded triangular shape, with no lips. Esophagus is short (830 µm in the Chabaud & Choquet females, 500 µm in the males), becoming wider posteriorly, nerve ring located just behind its anterior third. Excretory pore located at mid-esophagus, and two deirids found just posterior to the excretory pore.

Chabaud & Choquet (1955) noted that *Pararhabdonema* shares affinities with *Pseudostertagia bullosa* Ransom & Hall, 1912, a parasite of North American artiodactyls. However, it differs in the following features: vulva more anteriorly situated, esophagus shorter and thicker, latero-ventral ridges finer and longer than lateral ridges, and differences in the cuticular lobes beneath the cloaca. Gibbons & Khalil (1982) subsequently considered it a genus of "uncertain affinities" within Trichostrongylidae. Finally, Durette-Desset *et al.* (1999), based on a morphology-based cladistic analysis of Trichostrongyloidea, classified *Pararhabdonema* in the Libyostrongylinae (Family Cooperiidae), sister to *Laurostrongylus* and a clade containing *Libyostrongylus*, *Paralibyostrongylus*, and *Cnizostrongylus*. More recent works (Anderson, 2000) retain Libyostrongylinae but within the lumped family Trichostrongylidae.

Life cycle & mode of transmission – In related species (*Libyostrongylus* spp., *Paralibyostrongylus* spp.) eggs are passed in the fecal stream, hatch and develop into infective third-stage larvae during several days in the environment, with infection occurring through ingestion of third-stage larvae (Anderson, 2000).

Diagnosis at necropsy – Kreis (1945) gives no indication of the appearance or location of *Pararhabdonema longistriata* worms at necropsy. Chabaud & Choquet (1955) state only that worms were found in the stomach ("estomac").

Diagnosis in fecal examination – Based on closely-related species one would expect a fecal-oral direct transmission with mature or maturing eggs found in feces.

Hosts – Definitively described from adults in *Avahi laniger* (Kreis, 1945), *Lepilemur ruficaudatus* (Chabaud & Choquet, 1955), *Indri indri* (Chabaud *et al.*, 1961a), *L. microdon* (Chabaud *et al.*, 1965), *Varecia variegata* (Chabaud *et al.*, 1965), *Eulemur fulvus* (Chabaud *et al.*, 1965), *E. albifrons* (Chabaud *et al.*, 1965), *Propithecus coquereli* (Chabaud *et al.*, 1965), and *A. occidentalis* (Chabaud *et al.*, 1965). Faulkner *et al.* (2004) described *Pararhabdonema*-like eggs found in the feces of *I. indri*, *Hapalemur* spp., and *V. variegata*. Raharivololona (2006) found "trichostrongylid" eggs in *Microcebus murinus* feces

from Mandena. These eggs were ovoid with one rounded end and one blunt end. Though they match the general morphology of Trichostrongylidae, they differ from described *Pararhabdonema* eggs in having undifferentiated contents, and being slightly narrower (68 x 30 μm). Thus, it is unclear whether these eggs were produced by *P. longistriata*, or an undescribed species.

Chabaud *et al*. (1965) noted that *Pararhabdonema longistriata* is widespread throughout the different regions of Madagascar but is generally found only in the most folivorous lemurs: Indriidae (*Indri indri*, *Propithecus* spp., and *Avahi* spp.). The records they note for the frugivorous *Eulemur* derived only from two captive animals, which had few worms (one had under-developed worms in the stomach, the other a single worm in a blister on the muzzle). However, the record in *Varecia variegata* appeared to be a normal infection in a wild animal. The more recent records in *V. variegata* (a frugivore), *Hapalemur* spp. (bamboo specialists), and *Microcebus murinus* (an omnivore), if *Pararhabdonema*, are exceptions to this general trend (Faulkner *et al*., 2004; Raharivololona, 2006).

Clinical signs – None recorded.

Order Oxyurida
 Superfamily Oxyuroidea
  Family Oxyuridae
   Subfamily Enterobiinae
    ***Lemuricola* (8 species)** Chabaud & Petter, 1959

History – The pinworm parasites of lemurs include eight *Lemuricola* spp., which were originally described within three genera. Baer (1935) described *Enterobius lemuris* from *Eulemur albifrons* and *E. macaco*, and Sandosham (1950) described additional specimens from a captive *E. macaco*. Chabaud & Petter (1958) provided additional figures and documented the same species in *E. macaco* from Nosy Be. In examining additional pinworm specimens, Chabaud & Petter (1959) subsequently described the new genus and species *L. contagiosus* from two captive animals: *Cheirogaleus major* (a Malagasy lemur) and *Galago senegalensis* (an African prosimian). The same species was later found in wild *C. major* (Chabaud *et al*., 1965), confirming earlier suspicions that *Cheirogaleus* was the original host and *Galago* was infected in captivity. Chabaud *et al*. (1961b) described the new genus and species *Biguetius trichuroides* from *Propithecus verreauxi* at Lamboromakandro. Chabaud *et al*. (1965) described *L.* (*Madoxyuris*) *vauceli* from *E. fulvus*, *L.* (*Madoxyuris*) *baltazardi*

from *E. fulvus*, and *Lemuricola* (*Madoxyuris*) *bauchoti* from *Hapalemur* sp. Petter *et al*. (1972) described *Lemuricola* (*Madoxyuris*) *daubentoniae* from *Daubentonia madagascariensis*. Finally, Hugot *et al*. (1995) named *L. microcebi* from specimens mentioned by Petter *et al*. (1972) originally collected from *Microcebus murinus*. The three described genera were subsequently reduced to one: Hugot *et al*. (1995, 1996) and Hugot (1999) moved *Enterobius lemuris* and *Biguetius trichuroides* to *Lemuricola* (subgenera *Madoxyuris* and *Biguetius*, respectively), and placed *Lemuricola* within the subfamily Enterobiinae.

There is one additional *Lemuricola* species with a host species outside Madagascar: *L.* (*Protenterobius*) *nycticebi* (Baylis, 1928), parasite of *Nycticebus coucang* (a southeast Asian prosimian). This species is not considered in the descriptions below.

Some binomials applied to pinworms of lemurs are no longer considered valid. *Buckleyenterobius dentata* Sandosham, 1950 is considered a synonym of *Lemuricola lemuris* (Chabaud *et al*., 1965). The name *Enterobius anthropopitheci* was applied to pinworms described from *Eulemur fulvus* from a zoological garden in India (Baylis & Daubney, 1922), but this is considered a parasite acquired in either captivity, or an assignment to the described species most closely matching the specimens (at that time, none of the Malagasy species had been named; Chabaud *et al*., 1965).

Thus, the currently accepted list of *Lemuricola* species is as follows (taxonomy after Hugot, 1999):

Lemuricola (Biguetius) trichuroides (Chabaud *et al*., 1961)

Lemuricola (Lemuricola) contagiosus Chabaud & Petter, 1959

Lemuricola (Lemuricola) microcebi Hugot *et al*., 1995

Lemuricola (Madoxyuris) baltazardi Chabaud, Brygoo & Petter, 1965

Lemuricola (Madoxyuris) bauchoti Chabaud, Brygoo & Petter, 1965

Lemuricola (Madoxyuris) daubentoniae Petter *et al*., 1972

Lemuricola (Madoxyuris) lemuris (Baer, 1935)

Lemuricola (Madoxyuris) vauceli Chabaud, Brygoo & Petter, 1965

Morphology – Species in this group vary greatly in body length (from 1 to 22 mm), but are united by a suite of common features. The mouth is triangular and bordered by three equal-sized lips, one dorsal and two latero-ventral. External circle of four or eight papillae; internal circle of papillae sometimes present.

In some species (subgenus *Madoxyuris*), the lips are extended by a thin, transparent membrane projecting anteriorly. Behind the three lips are three (occasionally six or zero) corresponding esophageal teeth in a small, simple buccal cavity. Esophagus is simple, with (from front to back) a poorly-defined pharynx, long corpus (widening posteriorly), a short isthmus (narrowing), and a round esophageal bulb with a valvular apparatus. Nerve ring anteriorly placed, in the anterior third of the esophagus. Excretory pore may be between the level of the posterior widening of the esophageal corpus up to just posterior to the esophageal bulb, depending on species. All species have lateral alae; in some there are two pairs in the posterior part of the body.

Females: Vulva located roughly mid-way between anterior extremity and anus. Tail is long, as is typical of pinworms (14-50% body length) and can be thin and pointed, or conical (depending on the species). Vulva sometimes overhanged by a cuticular swelling, its opening oriented posteriorly. The genital apparatus consists of paired ovaries and uteri opening into a common chamber, which in turn opens up into a muscular vagina. The vagina usually runs anteriorly from the vulva (in contrast to *Enterobius*), though this may become obscured or altered in gravid females.

Males: Cuticle is ornamented by a series of transverse striations ("area rugosa") along the ventral midline, which may be superimposed on a thick midline cuticular ridge. The single spicule is transparent, similar to *Enterobius*. There is a "caudal point" in some species. There are small caudal wings near the cloaca, but no large copulatory bursae. Several pairs of large papillae surround the cloaca (usually 3 pairs, of which one is anterior and two posterior to the cloaca). The two postcloacal pairs are surrounded by a distinctive, transversely-oriented, roughly rectangular chitinous plate (lacking in *Enterobius*); this is only partially developed in some species.

Within *Lemuricola*, subgenera and species are mainly differentiated by: (1) adult size, (2) relative esophagus length, (2) tail length in females, (3) presence/absence of a caudal point in the male, and (4) male pericloacal anatomy (especially the development of the postcloacal chitinous plaque, and arrangement of papillae).

The three subgenera can be readily distinguished by several defining features. Within the subgenus *Lemuricola*, males have a long caudal point and well-developed postcloacal chitinous plate. Within the subgenus *Madoxyuris*, males lack a caudal point, with cloacal overture in an upside-down "Y"-shaped slit, and poorly-developed postcloacal chitinous plate. The subgenus *Biguetius* (for which the male is unknown) is distinct in having an extremely long tail in the female (50% of body length). All species and some diagnostic measurements are listed in Table 1.

Life cycle & mode of transmission – Unstudied. In related species (*Enterobius vermicularis*) female worms develop eggs in utero, then migrate to the anus of the host to deposit eggs in the perianal region or perineum (Anderson, 2000). Larvae molt inside the eggs and reach the infective stage (eggs containing third-stage larvae) within hours. Infection in lemurs may be through direct grooming of the perianal region, or through olfactory inspection of scent marks (J. Loudon, pers. comm.; scent marking lemurs rub their perianal region on substrates such as branches). Some eggs may hatch on the anal mucosa and the larvae reinvade the original host (retrofection).

Diagnosis at necropsy – Chabaud & Petter (1958) noted that *Lemuricola lemuris* worms recovered at necropsy from *Eulemur macaco* were located in both the small and large intestines. Chabaud *et al.* (1961b) noted that *L. trichuroides* worms recovered at necropsy from *Propithecus verreauxi* were located in the "intestine". Hugot *et al.* (1995) note that *L. microcebi* and *L. contagiosus* worms were found in the caecum and colon of the hosts, *Microcebus murinus* and *Cheirogaleus major*, respectively. Other authors did not specify location of worms at necropsy.

Diagnosis in fecal examination – Based on closely-related species one would expect a fecal-oral direct transmission.

It is important to note that fecal examination might not be the best diagnostic tool for *Lemuricola*, as the females migrate out of the anus and lay their eggs directly on the perineum. When possible (i.e. during animal captures), researchers should directly harvest eggs from the perineum for diagnosis.

Eggs are of the typical pinworm shape, oblong and asymmetrical (flattened on one surface; Figure 4). They may be embryonated or have undifferentiated contents, depending on the species and the method of collection. *Lemuricola* eggs can be differentiated from *Callistoura* eggs by their thin wall and lack of an operculum, but are morphologically similar to *Ingloxyuris inglisi* eggs and may be indistinguishable. The described eggs of the various species differ in both size and degree of embryonation, but these differences should be applied with caution when identifying eggs. Most morphological descriptions came from few adult specimens from one or few host

Table 1. Comparative morphometrics of eight species of *Lemuricola*.

	Length (mm) / width (µm) (♀)	Length (mm) / width (µm) (♂)	Eggs length/ width (µm)	Oesophagus length (% distance from anterior extremity to anus/cloaca)	Tail length of female (% body length)	References
L. (Biguetius) trichuroides	22 / 750	n/a	92 / 48	4.8 (♀)	50.0	(Chabaud *et al.*, 1961b)
L. (Lemuricola) contagiosus	4-5 / 400	2 / 200	95-105 / 35-45	15.2 (♀), 22.4 (♂)	29.8	(Chabaud & Petter, 1959)
L. (Lemuricola) microcebi	2.78 / 202	1.72 / 106	89 / 37	13.4 (♀), 16.7 (♂)	13.7	(Hugot *et al.*, 1995)
L. (Madoxyuris) baltazardi	5.3 / 420	3.15 / 220	70 / 30	16.2 (♀), 16.4 (♂)	15.1	(Chabaud *et al.*, 1965)
L. (Madoxyuris) bauchoti	2.85 / 200	1.2 / 80	57 / 23	20.1 (♀), 26.3 (♂)	19.3	(Chabaud *et al.*, 1965)
L. (Madoxyuris) daubentoniae	4.6 / 370	3.25 / 260	75 / 35	17.8 (♀), 18.5 (♂)	13.0	(Petter *et al.*, 1972)
L. (Madoxyuris) lemuris	5-6.6 / 440- 500 (Baer, 1935); 8 mm (Chabaud & Petter, 1958)	1.3-1.7 / 120-160 (Baer, 1935); 4.6 mm (Chabaud & Petter, 1958)	58-62 / 25-30 (Baer, 1935) 65 / 22 (Sandosham, 1950)	23.4 (♀), 26.1 (♂) (Baer)	19.0 (Baer)	(Baer, 1935; Sandosham, 1950; Chabaud & Petter, 1958)
L. (Madoxyuris) vauceli	5.3 / 310	2.8 / 200	65 / 28	35.8 (♀), 34.4 (♂)	23.6	(Chabaud *et al.*, 1965)

animals, and thus the range of variation and potential overlap is poorly known.

Hosts – Documented lemur host species (i.e. harboring adult worms at necropsy) for *Lemuricola* species are listed in Table 2.

In addition, *Lemuricola*-like eggs have been found in feces from the following taxa: *Eulemur* spp. (Faulkner *et al.*, 2004), *E. rubriventer*, *Lepilemur dorsalis*, and *L. edwardsi* (Junge & Sauther, 2006), *Propithecus deckeni deckeni* (Junge & Louis, 2005), *E. macaco* (Junge & Louis, 2007), *E. rubriventer*, *E. rufus*, *P. edwardsi*, and *L.* sp. (Hogg, 2002, in prep.; Wright *et al.*, 2009), and *Lemur catta* (Loudon *et al.*, 2006). Junge & Louis (2002) noted "pinworm" eggs in the feces of *Lepilemur mustelinus* and Schad *et al.* (2005) noted "Oxyuridae" eggs in *Microcebus murinus*; these eggs might represent *Lemuricola*, *Ingloxyuris*, or another taxon, as-yet undescribed in lemurs. Raharivololona (2006, 2009) described Oxyuridae-like eggs from *Cheirogaleus medius* (said to resemble *Heterakis*) and *M. murinus* (said to resemble *Enterobius*, *Lemuricola*, and *Syphacia*). However, given that (1) eggs are not readily diagnostic in this group, and (2) *Lemuricola* and *Ingloxyuris* are the only Oxyuridae documented to parasitize lemurs, the provisional genus designations should be regarded with caution.

The host specificity of individual species is impossible to assess given the small amount of data available. However, the genus as a whole parasitizes a wide range of lemurs, including frugivores (*Eulemur* spp.), mixed frugivore-folivores (*Propithecus*), bamboo specialists (*Hapalemur*), and hard-object feeders (*Daubentonia*).

Clinical signs – None recorded.

Order Oxyurida
Superfamily Oxyuroidea
Family Oxyuridae sensu lato
Ingloxyuris
Ingloxyuris inglisi Chabaud, Petter & Golvan, 1961.

History – Chabaud *et al.* (1961b) described the new genus and species *Ingloxyuris inglisi* from *Lepilemur ruficaudatus* at Beroboka. Chabaud *et al.* (1965) included *Ingloxyuris* as a subgenus of *Lemuricola*, but this was later reversed by Hugot *et al.* (1996) who removed it from *Lemuricola* and Enterobiinae, and placed it within Oxyuridae sensu lato.

Morphology – Chabaud *et al.* (1961b) described a female measuring 3.3 mm long, maximum width ~ 250 µm, and esophagus ~ 450 µm, and a male measuring 1.3 mm long, with maximum width ~ 70 µm, and esophagus ~ 310 µm.

The cephalic extremity has a collar of roughly 20 µm diameter ("peribuccal plateau"), formed by an uprising of the cuticle surrounding the mouth and roughly square in apical view (consisting of four equally-spaced angles). Eight sensory papillae (four medio-median and four latero-median) on the peribuccal plateau, two lateral amphids posterior to

Table 2. Lemur species reported as hosts of *Lemuricola* spp. (adult worms found at necropsy).

Parasite species	Host species and localities	References
L. (Biguetius) trichuroides	*Propithecus verreauxi* (Lamboromakandro)	(Chabaud *et al.*, 1961b)
L. (Lemuricola) contagiosus	*Cheirogaleus major* ("eastern forests"; in captivity for 4 years), *C. major* (Mahambo)	(Chabaud & Petter, 1959; Chabaud *et al.*, 1965)
L. (Lemuricola) microcebi	*Microcebus murinus* (captive)	(Hugot *et al.*, 1995)
L. (Madoxyuris) baltazardi	*Eulemur fulvus* (Ampijoroa)	(Chabaud *et al.*, 1965)
L. (Madoxyuris) bauchoti	*Hapalemur* sp. (Ambavaniasy)	(Chabaud *et al.*, 1965)
L. (Madoxyuris) daubentoniae	*Daubentonia madagascariensis* (Maroantsetra; in captivity for several weeks)	(Petter *et al.*, 1972)
L. (Madoxyuris) lemuris	*Eulemur albifrons*, *E. macaco*, *E. macaco* (Nosy Be)	(Baer, 1935; Sandosham, 1950; Chabaud & Petter, 1958; Chabaud *et al.*, 1965)
L. (Madoxyuris) vauceli	*Eulemur fulvus* (Ampijoroa/Ankarafantsika), *E. mongoz* (Ampijoroa), *Hapalemur* sp. (Ambavaniasy)	(Chabaud *et al.*, 1965)

the plateau. Mouth is large, circular, and contains nine chitinous teeth (6 external, 3 internal). Esophagus with (from front to back) a simple corpus (widening slightly posteriorly), a long isthmus (in contrast to *Lemuricola*), and a valvulated esophageal bulb. Nerve ring located at 50% esophageal length, excretory pore posterior to esophageal bulb. Lateral alae are present, extending from the esophageal bulb to the caudal region.

Females: Vulva anteriorly located (20% body length) and ovijector oriented posteriorly. Two uteri. Gravid females can have a body filled with eggs from the vulva almost to the anus. Tail is long (580 µm; 18% body length) and pointed.

Males: Cuticle is ornamented by striated cuticular crest along the posterior part of the ventral midline (roughly the posterior third of the body). The caudal extremity is rounded, about 40 µm from the cloaca. Three large pairs of pericloacal papillae (one anterior to the cloaca, two posterior). No chitinous plaque posterior to cloaca. An additional large pair of papillae is located at the caudal extremity. The single spicule (45 µm long) is lightly curved ventrally.

Life cycle & mode of transmission – Unstudied, most likely direct.

Diagnosis at necropsy – Chabaud *et al.* (1961b) noted that *Ingloxyuris inglisi* worms recovered at necropsy from *Lepilemur ruficaudatus* were located in the "last segments of the intestine".

Diagnosis in fecal examination – Based on closely-related species one would expect a fecal-oral direct transmission with eggs being passed in the feces.

Eggs are of the typical pinworm shape, oblong and asymmetrical (flattened on one surface), measure 70 x 28 µm and are embryonated when released (Chabaud *et al.*, 1961b). *Ingloxyuris* eggs can be differentiated

from *Callistoura* eggs by their thin wall and lack of an operculum, but are morphologically similar to *Lemuricola* eggs and may be indistinguishable.

Hosts – Adult worms of *Ingloxyuris inglisi* have been documented only from *Lepilemur ruficaudatus* at three localities: Ampijoroa, Lamboromakandro, and Beroboka (Chabaud *et al.*, 1961b, 1965). No subsequent studies have documented *Inglisoxyuris* eggs from fecal examinations. However, it is possible that some researchers documenting "*Lemuricola*" or "pinworm" eggs might have in fact seen *Ingloxyuris*, especially within *Lepilemur* species: for example, *L. dorsalis*, *L. edwardsi*, and *L. mustelinus* (Junge & Louis, 2002; Junge & Sauther, 2006).

Based on the limited available data, *Ingloxyuris inglisi* appears to be specific to *Lepilemur* spp. Since no *Lemuricola* have definitively been described from *Lepilemur*, it is possible that these two helminth genera have an allopatric host distribution, with *Ingloxyuris* parasitizing *Lepilemur* and *Lemuricola* parasitizing most or all other lemur genera.

Clinical signs – None recorded.

Order Oxyurida
 Superfamily Oxyuroidea
  Family Pharyngodonidae
   Callistoura
    Callistoura brygooi Chabaud & Petter, 1958
    Callistoura blanci Chabaud, Brygoo & Petter, 1965

History – This genus has two described species. Chabaud & Petter (1958) named the new genus and species *Callistoura brygooi* from adult worms found in the large and small intestines of a wild *Eulemur macaco* killed at Nosy Be in 1957. Chabaud *et al.*

(1965) named the second species *Callistoura blanci* from adult male worms found in a captive *E. albifrons* at Tsimbazaza and adult worms of both sexes found in a wild *E. fulvus* killed at Ampijoroa.

Chabaud & Petter (1958) note that *Callistoura brygooi* has a mixture of primitive and derived characteristics but suggested it is most similar to the genus *Oxyuris*. Chabaud *et al.* (1965) included *Callistoura* within Oxyuridae, but as *incertae sedis*; it was later placed within Pharyngodonidae by Petter & Quentin (1976).

Morphology – *Callistoura brygooi* - Chabaud & Petter (1958) described females measuring 9.8-14.1 mm long, maximum width ~ 620 µm, and esophagus ~ 590 µm. Males measured 6.5-8.4 mm long, with maximum width ~ 350 µm, and esophagus ~ 520 µm.

Cylindrical body with thick cuticle and transverse striae spaced ~ 22 µm apart in females and ~ 14 in males. Cuticle swollen to form a "cephalic hood" which is thickest at the anterior extremity and gets progressively thinner posteriorly, ending at the level of the posterior border of the esophagus. Large lateral wings start at the posterior border of the cephalic hood, and are well-defined throughout the length of the body until they disappear in the caudal region. Head is flat, with hexagonal mouth encircled by six lips arranged in three pairs (alternatively, three lips each with a median fissure). Two large, pronounced amphids, projecting farther than the lips, and four less-pronounced submedian sensory papillae. Esophagus bulged at anterior and posterior ends, with the anterior third well-differentiated and forming the pharynx, with nerve ring found just posterior to the pharynx. Posterior end is similar in structure to the middle third, and contains no sclerotized apparatus but only esophago-intestinal valves. Excretory pore well posterior to the esophagus.

Female has a long, pointed tail (~ 2.5 mm); vulva at 47% body length and its external opening is overhanged by a thick triangular appendix. Paired uteri, both anteriorly-directed. Eggs become mature on the way to the genital aperture.

Male has an extremely complex caudal extremity, with a caudal bursa almost as well-developed as in Strongylida. Lateral wings are dilated posteriorly and terminate just before the bursae, but there is an additional pair of "caudal wings" in the caudal region just dorsal to the lateral wings. The caudal bursa consists of two pairs of ventro-lateral wings, a central genital cone with three pairs of ventral digitations and a pair of lateral wings, and a dorsal caudal appendage. The spicule (~ 150 µm long) supports the genital cone and appears double but is a single spicule with a less-sclerotized median line (perhaps derived from a fusion of two spicules).

Morphology – *Callistoura blanci* - Chabaud *et al.* (1965) described a female measuring 10.6 mm long, maximum width ~ 540 µm, and esophagus ~ 530 µm. The male measured 4.3 mm long, with maximum width ~ 230 µm and esophagus ~ 400 µm. General morphology is similar to *C. brygooi* except: lateral wings much less-pronounced (terminating on the posterior quarter of the body), eight rather than four sensory papillae at the cephalic extremity, the external opening of the vulva more simple, male's genital cone is not supported by a spicule and the dorsal caudal appendage is shorter.

Life cycle & mode of transmission – Unstudied, but likely to be direct from ingestion of infective eggs.

Diagnosis at necropsy – Chabaud & Petter (1958) state only that adult *Callistoura brygooi* were found in both the small and large intestines of *Eulemur macaco* at necropsy. Chabaud *et al.* (1965) give no indication of the location of worms at necropsy.

Diagnosis in fecal examination – Based on closely-related species one would expect a fecal-oral direct transmission with mature eggs found in feces.

Based on examinations of gravid females (Chabaud & Petter, 1958; Chabaud *et al.*, 1965), *Callistoura brygooi* eggs measure 98 x 50 µm and *C. blanci* eggs measure 100 x 48 µm. The eggs are flattened on one face (as for Oxyuridae), but can be recognized based on two diagnostic features. First, they have very thick (2-3 µm), striated shells. Second, one end has small bumps and the other has an obliquely-placed operculum (in *C. brygooi* the eggs are embryonated at an advanced stage of development, with the caudal extremity of the larva always occupying the operculated end of the egg). Figures in the original publications indicate that *C. brygooi* eggs are fully embryonated, while those of *C. blanci* have undifferentiated contents. This could provide a means for distinguishing the two species in fecal examinations, but this has yet to be explicitly tested.

Hosts – *Callistoura brygooi* has been definitively described from adult worms in *Eulemur macaco macaco*, *E. fulvus*, and *Indri indri* (Chabaud & Petter, 1958; Chabaud *et al.*, 1965). *Callistoura blanci* has been definitely described from adult worms in *E. albifrons*, *E. fulvus*, and *Indri indri* (Chabaud *et al.*, 1965).

Faulkner *et al.* (2004) found *Callistoura*-like eggs in *Eulemur* spp. and *Varecia variegata*. Hogg (2002, in prep.) recorded *C. brygooi*-like eggs in *E. rubriventer*, *E. rufus*, *V. variegata*, and *Hapalemur aureus*. Junge & Sauther (2006) additionally report *Callistoura*-like eggs from *Lepilemur dorsalis*. Junge & Louis (2007) recorded *Callistoura*-like eggs from *E. macaco* from Lokobe. S. K. Martin (pers. comm., 2006) identified *Callistoura*-like eggs in the feces of *E. albocollaris* from Manombo Special Reserve and Mahabo Classified Forest (Figure 4).

Chabaud *et al.* (1965) note that these two species seem to have a very broad distribution throughout the island of Madagascar, yet no obvious specificity to a particular kind of lemur host (*Eulemur* spp. are among the most frugivorous lemurs, *Indri* is highly folivorous).

Clinical signs – None recorded.

Order Ascaridida
 Superfamily Subuluroidea
  Family Subuluridae
   Subulura
    Subulura baeri Chabaud, Brygoo & Petter, 1965

History – Chabaud *et al.* (1965) described the new species *Subulura baeri* from *Microcebus murinus* at Ampijoroa. The previously described species *S. prosimiae* (Baer, 1935), documented from a captive *Eulemur fulvus* in Hamburg, was later considered a synonym of *Primasubulura distans*, a commonly-acquired infection transmitted among primates (Chabaud *et al.*, 1965). A second species previously documented in a *Cheirogaleus* sp. captive in Paris (Chabaud & Petter, 1958), *S. otolicni*, is now considered a parasite acquired in captivity (it is otherwise known from *Galago* species in Africa) (Chabaud *et al.*, 1965).

Morphology – Chabaud *et al.* (1965) described a female measuring 16.1 mm long, maximum width 370 µm, and esophagus 2.2 mm, and a male measuring 11.2 mm long, with maximum width 290 µm, and esophagus 1.8 mm.

The mouth is circular and slightly larger than the buccal cavity. Anterior border of the buccal cavity has many fine incisions and forms a ring of roughly 125 elements. Pharynx muscular and with helical internal structure. Mouth surrounded by two large lateral amphids, four large external submedian papillae and six small papillae around the buccal border. No cervical wings, but cuticle slightly inflated laterally from the anterior extremity to the end of the pharynx.

Nerve ring and excretory pore anteriorly located (14% and 21-23% esophageal length).

Females: Vulva located at 48% body length. Tail is 1.05 mm (6.5% body length).

Males: Tail short (270 µm; 2.4% body length). Gubernaculum present (length 150 µm), two equal-sized spicules (length 980 µm). Pericloacal region has 10 pairs of papillae arranged from anterior to posterior, and two phasmids.

Life cycle & mode of transmission – Unstudied. In congeners gravid females produce thick-shelled, larvated eggs, which pass in the fecal stream. These eggs are consumed by an insect intermediate host, where they hatch and develop into encapsulated larvae. Lemurs are presumably infected when eating an insect intermediate host (Anderson, 2000).

Diagnosis at necropsy – Chabaud *et al.* (1965) give no indication of the appearance or location of *Subulura baeri* worms at necropsy.

Diagnosis in fecal examination – Lemurs would be expected to shed eggs in their fecal stream. Eggs are ovoid, measure 80 x 50 µm and embryonated (Chabaud *et al.*, 1965).

Hosts – Adult worms of *Subulura baeri* have been documented from *Microcebus murinus* at Ampijoroa and Mananara, and *Cheirogaleus medius* at Ampijoroa (Chabaud *et al.*, 1965). No subsequent studies have described either adults from necropsy or eggs from fecal examination. Raharivololona (2006, 2009) reported nematode eggs resembling *Subulura* from *M. murinus* at Mandena. Based on the limited data available, this species may be specific to Cheirogaleidae, which would not be surprising as this family is the most insectivorous.

Clinical signs – None recorded.

Order Ascaridida
 Superfamily Ascaridoidea
  Family Ascarididae
   Ascaris
    Ascaris petiti Chabaud, Brygoo & Petter, 1964

History – Chabaud *et al.* (1964) described the new species *Ascaris petiti* from *Daubentonia madagascariensis* at Mahambo.

Morphology – Chabaud *et al.* (1964) described juvenile, non-gravid females (the first 8 cm long/1.8 mm wide, and the second 6.2 cm long) and apparently adult-sized males (7 cm long, 1.8 mm wide, and 2.1 cm long/0.43 mm wide).
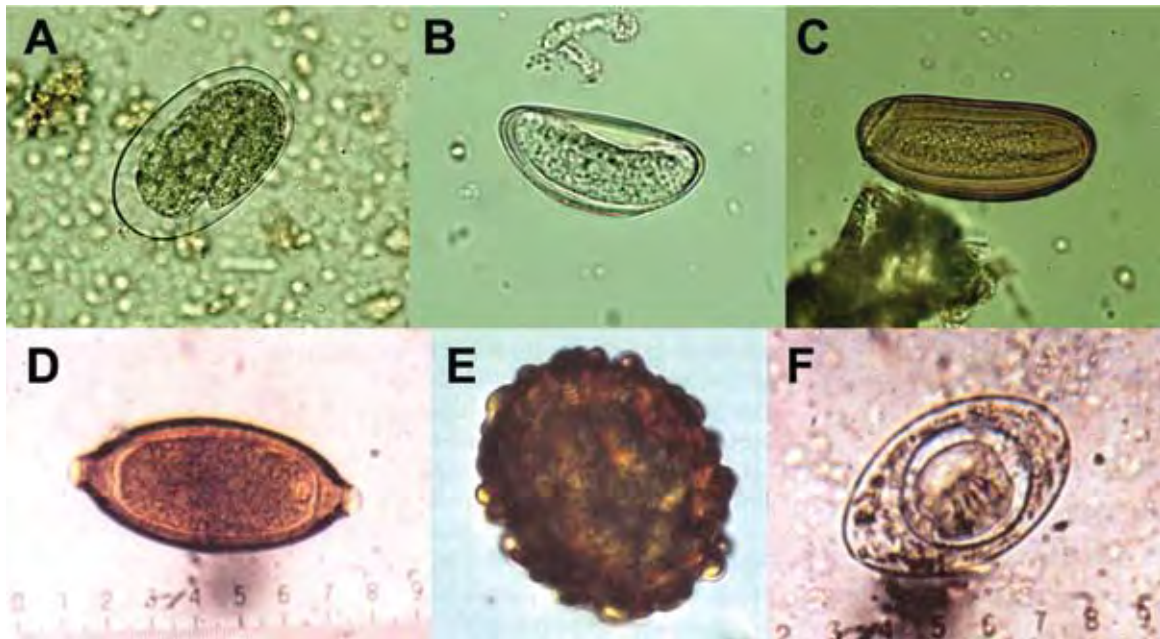
Figure 4. Examples of helminth eggs detected in fecal sampling. A) strongyle (Strongylida) parasite of *Propithecus diadema*, 78 x 47 μm. B) *Lemuricola* sp. parasite of *Eulemur albocollaris*, 60 x 27 μm. C) *Callistoura* sp. parasite of *E. albocollaris*, 99 x 41 μm. D) *Trichuris* sp. parasite of *Cheirogaleus medius* and *Microcebus murinus*, 85 x 40 μm. E) *Ascaris* sp. parasite of *M. murinus*, 65 x 45 μm. F) unidentified cestode (resembling *Hymenolepis*) parasite of *C. medius* and *M. murinus*, 55-65 x 40-55 μm. Sources: A: M. Irwin/J.L. Raharison; B-C: Courtesy S. Martin; D-F: courtesy B. Raharivololona.

Body is robust, with thick cuticle. Juveniles have weak lateral alae, which become imperceptible in adult specimens. Mouth surrounded by three lips and with sensorial apparatus identical to other *Ascaris*. Each lip is composed of two short lobes, each in turn subdivided into two parts by a midline fissure on the internal surface. Esophagus short and simple (7-10% body length), growing progressively thicker posteriorly. The nerve ring anterior to the excretory pore; both are anteriorly located (16-20% and 17-25% esophageal length). Deirids posterior to excretory pore and very small.

Females: Vulva located at 58-63% body length. Tail is 9-10% body length.

Males: Tail short (0.6-1.0% body length). Caudal region is simple, with numerous pericloacal papillae and paired spicules of 1.15 mm length (in the 7 cm male).

Life cycle & mode of transmission – Unknown. In congeners (*Ascaris lumbricoides*, *A. suum*) the host is infected by ingesting embryonated eggs. These eggs hatch in the intestine and the larvae pass through the gut wall and the hepatic portal system to the liver, lungs and up the trachea where they are swallowed. These larvae reach maturity and reproduce in the intestine; eggs are passed in the fecal stream (Anderson, 2000).

Diagnosis at necropsy – Chabaud *et al.* (1964) give no indication of the appearance or location of *Ascaris petiti* worms at necropsy.

Diagnosis in fecal examination – Based on closely-related species one would expect to find mature or maturing eggs in feces. Eggs were not described by Chabaud *et al.* (1964), since they examined only immature females. One might expect eggs to resemble other *Ascaris* species (*A. suum*, *A. lumbricoides*): embryonated, rounded (width almost equal to length), with thick brown shell, measuring 50-75 x 35-60 μm (Anderson, 2000).

Hosts – Adult worms of *Ascaris petiti* have been documented only from *Daubentonia madagascariensis* at Mahambo (Chabaud *et al.*, 1964, 1965). No subsequent studies have described either adults from necropsy or eggs from fecal examination.

Clinical signs – None recorded.

Order Spirurida

 Superfamily Spiruroidea

  Family Spiruridae

  Spirura

    Spirura diplocyphos Chabaud, Brygoo & Petter, 1965

History – Chabaud *et al.* (1965) described the new species *Spirura diplocyphos* from *Cheirogaleus medius* at Ampijoroa.

Morphology – Chabaud *et al.* (1965) described an immature female measuring 21 mm long, maximum width 390 µm, and esophagus 6.4 mm, and a male measuring 18 mm long, with maximum width 300 µm and esophagus 5.5 mm.

Head and mouth typical for the genus. Mouth highly chitinous, with two lateral pseudo-lips anteriorly (with amphids at the base) and six doubled denticles in the buccal cavity. Four small papillae at the border of the mouth, four larger papillae posteriorly. Pharynx laterally compressed, esophagus long (30-31% body length). Nerve ring very anteriorly placed (at the level of the muscular esophagus; ~ 1% body length), excretory pore at the level of the transition between the muscular and glandular esophagus (~ 2% body length). Both sexes have a diagnostic doubled cuticular ventral bossing (left-right pair) at 6-7% body length. Lateral alae extend from the nerve ring to the posterior border of the esophagus.

Females: Vulva located at 67% body length from the anterior end (note: an error in the original description makes this unclear). Ovijector oriented posteriorly. The tail is short (1% body length) with roughly ten short chitinous spines in a clump at the tip.

Males: Caudal extremity with large caudal alae, 750 µm high, 21 pericloacal papillae. Gubernaculum present, in the form of a flattened V, very thick and 95 µm tall. Paired, slightly rugose spicules (left: 350 µm, right: 240 µm). Short tail (2% body length).

Life cycle & mode of transmission – Unstudied. In congeners, adult worms live in the esophagus and stomach of the definitive host. Gravid females produce thick-shelled, larvated eggs, which pass in the fecal stream. These eggs are consumed by an insect intermediate host, where they hatch and develop into encapsulated larvae. Lemurs are presumably infected when eating the intermediate host (Anderson, 2000).

Diagnosis at necropsy – Chabaud *et al.* (1965) note only that the *Spirura diplocyphos* worms examined were discovered in the stomach of *Cheirogaleus medius* at necropsy.

Diagnosis in fecal examination – Based on closely-related species one would expect to find mature eggs in feces. Eggs are not described by Chabaud *et al.* (1965), since they examined only immature females. Eggs of other *Spirura* species are oval,

smooth-shelled and contain a first-stage larva with a prominent cephalic hook (Anderson, 2000); the eggs of *S. tamarini*, parasite of an Amazonian primate, measured 54-60 x 30-49 µm (Cosgrove *et al.*, 1963).

Hosts – Adult worms of *Spirura diplocyphos* have been documented only from *Cheirogaleus medius* and *Microcebus murinus*, both at Ampijoroa (Chabaud *et al.*, 1965). No subsequent studies have described either adults from necropsy or eggs from fecal examination. Based on the limited data available, this species may be specific to Cheirogaleidae, which would not be surprising as this family is the most insectivorous.

Faulkner *et al.* (2004) documented "Spiruroidea" larvae in *Daubentonia madagascariensis*; this could represent *Spirura*, *Rictularia*, or another taxon, as-yet undescribed in lemurs.

Clinical signs – None recorded.

Order Spirurida
 Superfamily Rictularioidea
 Family Rictulariidae
 Rictularia
  Rictularia lemuris Chabaud & Brygoo, 1956

History – Chabaud & Brygoo (1956) described the new species *Rictularia lemuri* from *Microcebus murinus* at Manakara, held in captivity for five months. A second species, *R. alphi* was documented in *Cheirogaleus* sp. and *Eulemur macaco* captive in Paris; this species was never documented in the wild and is now considered an infection likely acquired in captivity (Chabaud *et al.*, 1965).

Morphology – Chabaud & Brygoo (1956) described three immature females measuring 10 – 15.5 mm long. The largest specimen had maximum width 500 µm.

Anterior portion of the body thin, posterior third wider. Rounded cephalic extremity, with a slightly dorsally-oriented mouth. Buccal opening rounded-triangular, with seven small teeth along the dorsal border and three to four larger teeth along the latero-ventral borders. Buccal cavity wide, chitinous and relatively short, with three large esophageal teeth at the bottom. Fourteen papilla circling the mouth: six large papillae in an internal ring, each surrounded by moon-shaped cuticular features, and eight smaller papillae in an external ring. Two lateral amphids. Nerve ring and excretory pore anteriorly placed (2.2 and 3.3% body length). Esophagus 4 mm long (26%

body length), ending with three large valves. Tail is short (1.3% body length) and conical.

Two long, lateroventral rows of cuticular spines (each containing 83 spines) starting just below the buccal cavity and ending 1.3 mm before the caudal extremity. The 29 anterior spines are inter-locked, the remainder free. Spines reduced and more widely-spaced in the region of the vulva.

Vulva just anterior to the posterior border of the esophagus (25% body length) and opening within a marked cuticular depression. The cuticle in the region of the vulva (between the rows of spines) is marked with several spots.

Life cycle & mode of transmission – Unstudied. In congeners adult worms live in the intestine of the definitive host, either freely in the lumen or attached to the mucosa. Gravid females produce thick-shelled, larvated eggs, which pass in the fecal stream. These eggs are consumed by an insect intermediate host, where they hatch and develop into encapsulated larvae. Lemurs are presumably infected when eating the intermediate host (Anderson, 2000).

Diagnosis at necropsy – Chabaud & Brygoo (1956) note only that the *Rictularia lemuris* worms examined were discovered in the "digestive tube" of *Microcebus murinus*.

Diagnosis in fecal examination – Based on closely-related species one would expect to find mature eggs in feces. Eggs are not described by Chabaud *et al.* (1965), since they examined only immature females. One might expect eggs to resemble other *Rictularia* species: oval, larvated, and with smooth thick-walled shells (Anderson, 2000); eggs of *R. dipodomis*, parasite of the kangaroo rat, measure 46 x 30 μm (Tiner, 1948).

Hosts – Adult worms of *Rictularia alphi* have been documented only from *Microcebus murinus*, both in captivity (but deriving from Ampijoroa) and in the wild at Ampijoroa (Chabaud & Brygoo, 1956; Chabaud *et al.*, 1965). No subsequent studies have described either adults from necropsy or eggs from fecal examination. Based on the limited data available, this species may be specific to *Microcebus* or Cheirogaleidae, which would not be surprising as these lemurs are the most insectivorous.

Clinical signs – None recorded.

Order Spirurida
Superfamily Filarioidea
Family Onchocercidae
  Dipetalonema
    Dipetalonema petteri Chabaud & Choquet, 1955

History – Chabaud & Choquet (1955) described the new species *Dipetalonema petteri* from a *Lepilemur ruficaudatus* that had lived in captivity in Paris for one month. A suggestion that this species might be synonymous with the human filaria *Wuchereria bancrofti* var. *vauceli* (Chabaud & Brygoo, 1958), based on similarities of the microfilaria, was later abandoned (Chabaud *et al.*, 1965).

Chabaud *et al.* (1961b) note that a similar specimen has been described from lemurs (*Filaria lepilemuris* Fourment, 1883), which is probably synonymous with either *Dipetalonema petteri* or *Paulianfilaria pauliani*, but they reserve judgment until the type material has been located.

Morphology: Adults - Chabaud & Choquet (1955) described female adults. Body length 44 mm, with thin cuticle. Cephalic region narrow, body suddenly widening at the level of the vulva and attaining rapidly a maximum width of 480 μm. Head rounded, smooth, with very small, circular mouth. Four small medio-median papillae, four larger latero-median papillae. Amphids slightly anterior to level of latero-median papillae. A chitinous ring 10 μm long is found at the anterior border of the esophagus. Esophagus 1.3 mm long (3% body length), straight and without differentiated glandular part. Nerve ring and excretory pore anteriorly located (270 μm and 350 μm from anterior extremity). Deirids not identified. Tail 500 μm long (1% body length), blunt-tipped and narrowing slightly posteriorly, with four small papilliform projections at the tip (the dorsal pair appear to be phasmids), reminiscent of the caudal lappets seen in *Dipetalonema*.

Vulva anteriorly located (630 μm from anterior extremity; 1.5% body length), small and non-salient. Ovijector (vagina) 2 mm long and 100 μm wide, with a proximal sphincter and a tube posterior to the vulva and occasionally looped on itself, opening into a thin-walled chamber which gives rise to two uteri. Both uteri continue posteriorly (in parallel), ending 4 mm from posterior extremity, after which the oviducts (2.5 mm long) and ovaries (12 mm long) are convoluted.

Morphology: Microfilariae – Length 285 μm, width 5 μm in the anterior half of the body, progressively thinning in the posterior half. No sheath. Transverse striations visible on the cuticle near the anus.

Numerous small, somatic cellules. Cephalic space 8 μm long. Nerve ring, excretory pore, and cellule at 58, 70, and 90 μm from the anterior extremity. At mid-body (155-175 μm), contains reddish grains and scarce somatic cells. Rectal cells at 190 μm, anal cells at 225 μm. Caudal point is narrow, with last nucleus 10 μm from tail tip.

Life cycle & mode of transmission – Unstudied. In congeners, adults live in the thoracic and abdominal cavity of the definitive host, with gravid females releasing motile microfilaria rather than eggs, which migrate to the blood. Microfilariae are ingested by blood-sucking insects or other arthropods and develop in the intermediate host. After development is complete the infective-stage larvae migrate to the vector's mouthparts and emerge when it is biting another host, thus infecting a new definitive host (Anderson, 2000).

Diagnosis at necropsy – Chabaud & Choquet (1955) found approximately 60 adult female worms in the pleura and peritoneum and many microfilaria in blood recovered from the heart. No males were recovered from this individual, nor from the many individuals of several host species necropsied (see below); the cause for this bizarre phenomenon remains unknown.

Diagnosis in living animals – We would be expected for microfilariae to circulate in the blood of the infected lemur.

Hosts – Adult worms and microfilaria of *Dipetalonema petteri* have been documented from several host species: *Lepilemur ruficaudatus* from Ampijoroa and Beroboka, *Microcebus murinus* from Ampijoroa, *Eulemur macaco macaco* from Mahajanga, *E. fulvus* from Ampijoroa, *E. albifrons* from Bay of Antongil, *E. rufus* of unknown provenience, *E. mongoz* from Ampijoroa, *Propithecus coquereli* from Ampijoroa, and *Avahi occidentalis* from Ampijoroa (Chabaud & Choquet, 1955; Chabaud *et al.*, 1965). Finally, Junge & Louis (2005) recorded microfilariae matching the morphology of *Dipetalonema* in *P. deckeni deckeni* at Tsiombikibo.

The long and varied list of host species implies that this parasite has low host specificity. Chabaud *et al.* (1965) noted that its occurrence in the wild in western Madagascar (Ampijoroa, Mahajanga) is well-established, but its occurrence in the east (i.e. Bay of Antongil) is uncertain because the animal from this site was held in captivity for five months before its death and might have been infected in captivity.

Order Spirurida
Superfamily Filarioidea
Family Onchocercidae
Paulianfilaria Chabaud, Petter & Golvan, 1961
Paulianfilaria pauliani (Chabaud & Petter, 1958)

History – Chabaud & Petter (1958) described the new species *Dirofilaria pauliani* from a single specimen obtained from *Propithecus verreauxi* from Behara. Chabaud *et al.* (1961b) described eight additional specimens (3 male, 5 female) and created a new genus, *Paulianfilaria*, with *P. pauliani* designated as type species.

Chabaud *et al.* (1961b) noted that a similar specimen has been described from lemurs (*Filaria lepilemuris*), which is probably synonymous with either *Dipetalonema petteri* or *Paulianfilaria pauliani*, but they reserve judgment until the type material can be located.

Morphology: Adults – Chabaud *et al.* (1961b) described adult males of length 23-29 mm and females of length 62-65 mm, slightly smaller than the female type specimen at 78 mm and width 78 μm (Chabaud & Petter, 1958). Cuticle thick, with fine and closely-spaced transverse striae. Head rounded with very small, circular mouth. In apical view, the head has an anterior peribuccal square, of which each angle is occupied by a medio-median papilla, and a posterior circular region bearing the four latero-median papillae. No teeth or lips; chitinous ring at the anterior border of the esophagus (height 5 μm, diameter 22 μm). Esophagus straight and undifferentiated, 1.125 mm long (1.4% body length) in the female, 1.2 mm (5% body length) in the male. Nerve ring and excretory pore anterior (0.4-1.2% and 0.6-2.4% body length).

Female: Vulva posteriorly located (71% body length), with a fissure at its opening. Ovejector travels anteriorly from vulva until reaching 0.5-1 mm posterior to the esophagus, at which point it turns posteriorly and gives rise to a chamber filled with microfilaria. At around the level of the vulva, this chamber gives rise to two uteri. Tail short (420 μm; 0.5% body length), blunt-tipped and conical.

Male: Lateral lines 43 μm wide, tail 165 μm long (0.7% body length). Posterior extremity without lateral alae, ventral cuticle in the posterior region ornamented with fine transverse striae. No gubernaculum, two spicules (left: 375 μm long and thin, right: 125 μm, thick and concave). Seven pericloacal papillae: one large papillae just anterior to the cloaca, six smaller papillae along the posterior border of the pericloacal

ring. Two pairs of papillae at the posterior third of the tail, and a final pair at the terminus.

Morphology: Microfilariae – Chabaud *et al.* (1961b) described microfilariae taken from the uterus of the adult females examined. Average dimensions were: length 230 μm, width 4 μm, nerve ring, excretory pore and anal pore 50, 70 and 165 μm from anterior extremity.

Life cycle & mode of transmission – Unstudied. In other Onchocercidae adults live in the thoracic and abdominal cavity of the definitive host, with gravid females releasing live microfilaria rather than eggs, which migrate to the blood. Microfilariae are ingested by blood-sucking flies and develop in the intermediate host. After development is complete the infective-stage larvae migrate to the insect's mouthparts and emerge when it is biting another host, thus infecting a new definitive host (Anderson, 2000).

Diagnosis at necropsy – Neither Chabaud & Petter (1958) nor Chabaud *et al.* (1961b) give any indication of the appearance or location of *Paulianfilaria pauliani* worms at necropsy.

Diagnosis in living animals – Would expect to find microfilariae in either the blood or skin of infected lemurs.

Hosts – *Paulianfilaria pauliani* has been documented from *Lepilemur ruficaudatus* (Beroboka), *Propithecus verreauxi* (Lamboromakandro, Behara), and *P. coquereli* (Ampijoroa) (Chabaud & Petter, 1958; Chabaud *et al.*, 1961b, 1965). Chabaud *et al.* (1965) further noted that it is found in almost every *Propithecus* individual necropsied, but only once in *Lepilemur*. The two genera documented as hosts to date are not closely related, but are both relatively folivorous.

Order Spirurida
 Superfamily Filarioidea
  Family Onchocercidae
   Courduriella
    Courduriella courdurieri Chabaud, Brygoo & Petter, 1961

History – Chabaud *et al.* (1961a) described the new genus and species *Courduriella courdurieri* from adults and microfilaria in *Indri indri*.

Morphology: Adults – Chabaud *et al.* (1961a) described an adult female of length 71 mm and width 350 μm and males of length 21 mm and width 125 μm. Body is pointed at both ends, cuticle thin with fine and closely-spaced transverse striae. Anterior extremity extremely narrow (< 30 μm). Head and mouth not described in detail. Esophagus straight, thin and undifferentiated, 520 μm long (0.7% body length) in the female, 400 μm (1.9% body length) in the male. No chitinous ring at anterior end of esophagus. Nerve ring and excretory pore (which opens at a cuticular eminence) extremely anterior (0.2-0.6% and 0.2-0.7% body length). Intestine wider than esophagus, with blackish granulations.

Female: Vulva anteriorly located (0.3% body length), with no cuticular features at its opening. Ovijector travels posteriorly from vulva and gives rise to a common chamber, which gives rise to two uteri filled with microfilaria (themselves continuing posteriorly, in parallel). Oviducts and ovaries located in the last 6 mm of the body. Tail short (130 μm; 0.2% body length), blunt-tipped with a slight narrowing at half its length and subterminal phasmids.

Male: Ventral cuticle in the posterior region ornamented with transverse striae, more pronounced than those on the rest of the body. Barely perceptible, ventro-lateral caudal alae.

Tail short (70 μm; 0.3% body length), blunt-tipped with a slight narrowing at half its length. Pericloacal papillae small: one papillae just anterior to the cloaca, five pairs around the lateral and posterior borders of the cloaca. One additional pair of papillae at the posterior third of the tail. One pair of phasmids, 10 μm from the apex. No gubernaculum, two spicules (left: 360 μm long, right: 95 μm and only lightly chitinous, both divided into two parts of roughly equal length).

Morphology: Microfilariae – Chabaud *et al.* (1961a) described three microfilariae measuring length 128-140 μm, width 4-5 μm, with nerve ring and excretory pore 35-38 and 45-49 μm from anterior extremity. Somatic granules small, but granule at posterior extremity large and separated from the nearest by 10 μm. Cuticle has pronounced transverse striae, especially posteriorly. No girdle.

Life cycle & mode of transmission – Unstudied. In other Onchocercidae adults live in the thoracic and abdominal cavity of the definitive host, with gravid females releasing live microfilaria rather than eggs, which migrate to the blood. Microfilariae are ingested by blood-sucking flies and develop in the intermediate host. After development is complete, the infective-stage larvae migrate to the insect's mouthparts and emerge when it is biting another host, thus infecting a new definitive host (Anderson, 2000).

Diagnosis at necropsy – Chabaud *et al.* (1961a) found three female and two male adult *Courduriella courdurieri* in a "perirenal tumor" of *Indri indri*. The antemortem appearance of the "tumor" cannot be verified since it was disturbed by the bullet that killed the lemur, causing a large hemorrhage. "Abundant" microfilariae were found in the blood.

Diagnosis in living animals – Microfilariae are likely to be found in skin snips or in the blood of infected lemurs.

Hosts – *Courduriella courdurieri* has been documented only once from *Indri indri* at Périnet (=Analamazaotra). It thus appears, based on available data, to have a restricted host preference.

Order Spirurida
 Superfamily Filarioidea
  Family Onchocercidae
  Protofilaria
    Protofilaria furcata Chandler, 1929

History – Chandler (1929) described the new genus and species *Protofilaria furcata* from adults recovered from a captive *Varecia rubra* in Calcutta. Anderson (1961) published a re- description of the same type material examined by Chandler. Finally, Chabaud *et al.* (1961a) described additional examples from wild *Hapalemur griseus*.

Morphology: Adults – Chandler (1929) and Anderson (1961) described females measuring 23-30 mm long, maximum diameter 325-330 μm and males measuring 13-15 mm long, maximum diameter 150-175 μm. Chabaud *et al.* (1961a) described an "almost complete" posterior fragment of an adult female of length 17 mm and a complete male of length 14 mm and width 170 μm. Both anterior and posterior extremities are tapered (e.g. width of a male's anterior extremity ~ 100 μm). Cuticle is transversely striated and thickened on the lateral surfaces of the anterior body. Head has extremely small mouth, eight submedian papillae and two lateral amphids. Esophagus straight, thin and undifferentiated, 825-980 μm long (3-4% body length) in the female and 910-920 μm long (6-7% body length) in the male. Anterior end of esophagus has pronounced but only lightly chitinous ring. Nerve ring anterior (1.0% body length in female, 1.9% in male). Excretory pore and deirids not detected.

Female: Vulva anterior (12% body length), vagina extends anteriorly but uteri and ovaries extend posteriorly to approximately the level of the anus.

Uteri are filled with hatched embryos (microfilariae). Tail short (272 μm; 1.2% body length), tail tip has a laterolateral cleft with phasmids within.

Male: Tail short (95-100 μm; 0.6-0.7% body length), with rounded tip and slight narrowing at half its length. Pericloacal papillae small and difficult to discern, Chabaud *et al.* (1961a) detected at least four pairs but Anderson (1961) counted 11. Two or three additional pairs of papillae on the ventral surface of the posterior half of the tail. Well-defined subterminal phasmids, laterally placed. No gubernaculum, two spicules (left: 98 μm long, right: 78 μm).

Morphology: Microfilariae – Anderson (1961) described microfilariae extracted from the uteri of preserved females of length 250-277 μm and width 5 μm. Chabaud *et al.* (1961a) described microfilariae measuring length 308 μm (range 260-335), width 6 μm, with nerve ring, excretory pore and excretory cellule 67, 89, and 118 μm from anterior extremity. Anal pore 55 μm from posterior extremity. Somatic granules very large and tightly packed. Anterior extremity has empty space of ~ 5 μm, posterior extremity has four granules in single file.

Life cycle & mode of transmission – Unstudied. In other Onchocercidae, adults live in the thoracic and abdominal cavity of the definitive host, with gravid females releasing live microfilaria rather than eggs, which migrate to the blood. Microfilariae are ingested by blood-sucking flies and develop in the intermediate host. After development is complete, the infective-stage larvae migrate to the insect's mouthparts and emerge when it is biting another host, thus infecting a new definitive host (Anderson, 2000).

Diagnosis at necropsy – Specimens described by Chandler (1929) and Anderson (1961) were recovered from the "thoracic cavity" of a *Varecia rubra* at necropsy; no additional description is given. Specimens described by Chabaud *et al.* (1961a), from a necropsy of a *Hapalemur griseus* from Périnet (=Analamazaotra), were found within six whitish, calcified tumors in the pleura and surface of the lungs. Adult *Protofilaria furcata* were found in convoluted tubes within the tumors; extraction was difficult and caused damage to several of the specimens. Some tumors consisted of a "shell" of a female cadaver in which living microfilaria were found; numerous microfilariae were found in the blood of the same individual.

Diagnosis in living animals – Microfilariae in blood.

Hosts – *Protofilaria furcata* has been documented from captive *Varecia rubra* (Calcutta), *Hapalemur griseus* (Périnet/Analamazaotra), and captive *Propithecus coquereli* (Antananarivo). Based on available data, this species appears to have a diverse group of host species.

Order Enoplida
 Superfamily Trichinelloidea
  Family Trichuridae
   Trichuris
    Trichuris lemuris Rudolphi, 1819

History – Rudolphi (1819) mentions "*Trichocephalus* [=*Trichuris*] *lemuris*", having examined a female specimen from the intestine of a *Eulemur mongoz* at the Vienna museum, but includes this species only as a "Species Dubia" and gave it no description other than to compare it to *Trichocephalus simiarum*. Chabaud *et al.* (1964) provided the first modern description of this species (including both sexes), based on specimens obtained at necropsy for five lemur species, and reinstated the name as a valid binomial.

Morphology – Chabaud *et al.* (1964) described a female from *Daubentonia madagascariensis* and a male from *Cheirogaleus major*; thus, the degree of sexual dimorphism should be viewed with caution because of the potentially differing conditions in the two hosts and potentially long phylogenetic separation. The female measured 36 mm long, maximum width 680 μm, and esophagus 22.3 mm, and a male measuring 17.5 mm long, with maximum width 300 μm and esophagus 9.9 mm.

General aspect typical of *Trichuris*: long, very narrow anterior esophageal region with stichosome esophagus (in this species, 38-43% of body length), thicker posterior body, and a pronounced, ventrally-curved distal spicule in males.

The female specimen has a "bacillary band" along its left lateral cuticle, starting 130 μm from the anterior extremity and ending near the distal end of the esophagus, and composed of cuticular vesicles. Genital anatomy of both sexes typical of the genus. The girdle around the spicule takes on a variable appearance according to the spicule's degree of protrusion, but it is covered with spines, which are slightly sharper at the basal portion relative to the distal portion.

Life cycle & mode of transmission – Unstudied. In congeners, eggs are passed in the fecal stream, embryonate in the environment and are consumed directly by the host. Eggs hatch in the small intestine,

then the larvae migrate to the large intestine and attach themselves to the mucosa (Anderson, 2000).

Diagnosis at necropsy – Chabaud *et al.* (1964) give no indication of the appearance or location of *Trichuris lemuris* worms at necropsy, but do mention that the infections in all five species examined were not heavy and only few worms were recovered. Based on the behavior of congeners, adults should be found with the anterior (narrow) end of the body embedded in the mucosa of the large intestine.

Diagnosis in fecal examination – Based on closely-related species one would expect to find mature or maturing eggs in feces. Eggs measure 55 x 26 μm (Chabaud *et al.*, 1964); though no description was made in the text, the egg in the figure appears to be of typical *Trichuris* morphology: lemon-shaped, with bipolar plugs.

Hosts – Adult worms of *Trichuris lemuris* have been documented from five lemur species: *Cheirogaleus major* and *Daubentonia madagascariensis* from Mahambo, *Eulemur albifrons* from Bay of Antongil, and *E. fulvus* and *Lemur catta* in captivity at Antananarivo (Rudolphi, 1819; Chabaud *et al.*, 1964, 1965).

In addition, *Trichuris*-like eggs have been found in feces from the following taxa: *Eulemur* spp. (Faulkner *et al.*, 2004) and *E. fulvus rufus* (Junge & Louis, 2005). Schad *et al.* (2005) described both *Trichuris* and a second trichurid, *Trichosomoides*, from *Microcebus murinus*. Raharivololona (2006, 2009) described "*Trichuris*" eggs from *Cheirogaleus medius* and *M. murinus* (Figure 4), but also described "*Capillaria*" eggs from *M. murinus*. Neither *Trichosomoides* nor *Capillaria* have yet been described from adults in Madagascar; further analysis including recovery of adults is necessary to confirm the presence of these two genera.

Clinical Signs – None recorded.

2. Platyhelminthes
Class Cestoda
 Order Cyclophyllidea
  Family Anoplocephalidae
   Bertiella
    Bertiella lemuriformis Deblock & Capron, 1959

History – Deblock & Capron (1959) described the new species *Bertiella lemuriformis* from cestode fragments recovered from *Avahi laniger*. No subsequent study has documented adult worms.

Morphology - Deblock & Capron (1959) described several fragments including all parts of the body

length. Scolex non-pigmented, slightly flattened dorsoventrally (300-350 µm long x 310-410 µm wide). Four oval-shaped suckers, in two apposed pairs diametrically opposite one another, 130-210 µm in diameter (depending on state of contraction) and 110-150 µm deep. The muscular ring has a thickness of 32-48 µm. Suckers slightly raised from scolex surface but not pedestalled. When the scolex is stretched out or laterally compressed, the suckers are arranged two on the dorsal surface, two on the ventral surface. When the scolex is retracted, they are oriented anteriorly. There is no rostrum or internal skeleton.

Neck is short, almost as large as the head. Signs of segmentation first appear 130 µm from scolex, first well-defined segments at 160-180 µm. Proglottids get progressively larger posteriorly. Mature proglottids are imbricated, with one-third to one-half their length penetrating the base of the segment immediate anterior. The most complete specimen examined was 60 mm in length, with 444 proglottids and a maximum width of 4.5 mm. Proglottids are trapezoidal, very long relative to their width (the most posterior proglottids measured 300-375 µm long and 4,500 µm wide, with a thickness up to 450 µm. Cuticle is thick and lacks papillae. Each proglottid has two parallel excretory canals.

One genital pore per proglottid, positioned laterally in the middle of the lateral border. The side varies, with no more than three sequential proglottids having the pore on the same side. Each proglottid has a female and male reproductive system, with 40-50 testicles each (for more detail, see Deblock & Capron, 1959). Uterus restricted to the central portion of the proglottid. The sexual maturity of proglottids increases posteriorly, with eggs appearing in the 260th segment (23 mm from the scolex). Eggs measure 35-40 µm in diameter (Deblock & Capron, 1959) and are of the typical Anoplocephalan morphology. Shell composed of three concentric envelopes. Eggs contain a single hexacanth embryo 13-18 µm in diameter with hooks 7-8 µm long, enclosed in a pear-shaped "piriform apparatus".

Life cycle & mode of transmission – Unstudied. Anoplocephalids in general follow an indirect life cyle, invertebrates as intermediate hosts (Bowman, 2003). Eggs are shed in the feces of the definitive host, and consumed by invertebrates, in which they hatch and develop into cysticercoids. The definitive host is infected upon inadvertently consuming the intermediate host. For *Bertiella*, the intermediate host is an oribatid mite (Bowman, 2003).

Diagnosis at necropsy – Deblock & Capron (1959) gave no details of the way in which the *Bertiella lemuriformis* fragments were obtained, or their location at necropsy.

Diagnosis in fecal examination – Based on other anoplocephalans, one would expect to see single eggs in microscopic examination of feces and/or proglottids in macroscopic examinations.

Hosts – *Bertiella lemuriformis* has been documented from adult material only from *Avahi laniger*, of unknown provenience (Deblock & Capron, 1959). The genus *Bertiella* is widespread, with species infecting both anthropoid and prosimian primates, as well as marsupials, rodents, birds, and dermopterans.

Hogg (2002, in prep.) documented "Anoplocephalidae" eggs in *Propithecus edwardsi* at Ranomafana, provisionally identified as *Anoplocephala* and *Moniezia*. As these two genera produce eggs with a single embryo, their eggs should be similar to those of *Bertiella lemuriformis*; therefore, without recovering adults it is most conservative to conclude that these eggs might represent *B. lemuriformis* or a related species.

Junge & Sauther (2006) noted "cestode" eggs detected in the feces *Lemur catta* and *Propithecus candidus*, Loudon *et al*. (2006) recorded "tapeworms" from *L. catta* feces, and Raharivololona (2006) noted "cyclophyllidean" eggs in the feces of *Cheirogaleus medius* and *Microcebus murinus*. Without further information it is impossible to determine which taxon is represented (though the "cyclophyllidean" figured appears similar to *B. lemuriformis*).

Class Cestoda
 Order Cyclophyllidea
  Family Anoplocephalidae
   Thysanotaenia
    Thysanotaenia lemuris Beddard, 1911

History – Beddard (1911) described *Thysanotaenia lemuris* from two complete specimens and additional fragments from a *Eulemur macaco* living in captivity. Joyeux & Baer (1927) described additional specimens from *Varecia* sp., and Deblock & Diaouré (1962) described additional specimens and examined the possible synonymy of the genera *Thysanotaenia* and *Inermicapsifer*.

Morphology – Specimens up to 15 cm long. Scolex spherical, with no rostrum. Four suckers (diameter ~ 250-350 µm) in two opposed pairs, each pair facing laterally or anterolaterally. Diameter of scolex at level

of suckers 680 µm. Some black pigment posterior to suckers. Neck 1.5-3 mm, 360 µm wide. Stobila contains 150-200 proglottids, which lack posterior fringes. Anterior proglottids much wider than long, posterior proglottids roughly square (or slightly longer than broad). Mature proglottids differ from immatures in having greater thickness, longitudinal furrowing of their surface, and a dorsoventral constriction at mid-length (producing an hourglass-shaped outline in lateral view). Each proglottid has a single unilateral genital pore, in its anterior third, with a pronounced papilla marking its location. Beddard (1911) described an excretory system consisting of two longitudinal canals positioned bilaterally, but subsequent descriptions (Joyeux & Baer, 1927; Deblock & Diaouré, 1962) noted two pairs, with each side having a dorsal and ventral canal. Longitudinal canals are joined by a transverse canal at the posterior end of each proglottid. Cuticle is thick (6.5 µm), without ornamentation.

Each proglottid has a female and male reproductive system (for more detail, see Deblock & Diaouré, 1962). 100-190 testicles, in the dorsal part of the proglottid surrounding the ovary and usually confined to the posterior two-thirds of the proglottid, anterior to the transverse canal. Ovary has two digitated lobes, located near the proglottid's center (slightly on the side with the genital pore), and measures 450 x 600 µm. Mature proglottids contain numerous egg packets (~ 160 per proglottid). In the specimens examined by Deblock & Diaouré (1962), egg packets measure up to 130 µm in diameter, with 6-12 eggs inside measuring 26-38 x 26-29 µm. However, egg packets of specimens examined by Joyeux & Baer (1927) were larger: 300 x 150 µm, containing 5-6 eggs measuring 60 µm in diameter.

Both Joyeux & Baer (1927) and Deblock & Diaouré (1962) note the strong similarities between *Thysanotaenia lemuris* and *Inermicapsifer* (especially *I. madagascariensis*) in both general morphology and the appearance of the egg packets.

Life cycle & mode of transmission – Unstudied. Anoplocephalids in general follow an indirect life cyle, invertebrates as intermediate hosts (Bowman, 2003). Eggs are shed in the feces of the definitive host, and consumed by invertebrates, in which they hatch and develop into cysticercoids. The definitive host is infected upon inadvertently consuming the intermediate host.

Diagnosis at necropsy – Deblock & Diaouré (1962) noted that their study material derived from the small intestine of *Eulemur macaco*. Previous authors gave no details of the way in which the location or appearance of specimens at necropsy.

Diagnosis in fecal examination – Based on other anoplocephalans, one would expect to see egg packets in microscopic examination of feces and/or proglottids in macroscopic examinations.

Hosts – *Thysanotaenia lemuris* has been documented from adult material from *Eulemur macaco*, (Beddard, 1911; Deblock & Diaouré, 1962), *Varecia variegata*, and "*Lemur* sp." (probably *E.* sp. in current taxonomy) (Joyeux & Baer, 1927), all of unknown provenience within Madagascar.

Junge & Sauther (2006) noted "cestode" eggs detected in feces of *Lemur catta* and *Propithecus candidus* and Loudon *et al.* (2006) recorded "tapeworms" from *L. catta* feces; without further information it is impossible to determine which taxon is represented.

Class Trematoda
Order Digenea
Family Dicrocoeliidae
Zonorchis microcebi Richard, 1965

History – Richard (1965) described *Zonorchis microcebi* from 20 adult specimens from *Microcebus murinus*. No subsequent studies have documented adults of this species or any Trematoda from any other lemur species.

Morphology – Long spindle-shaped body (1.9-3.2 mm), with its widest point (760-860 µm) behind the ventral sucker. Oral sucker small and terminal, ventral sucker larger (diameter roughly 125-150% that of oral sucker) and situated in the anterior quarter of the body. Esophagus 120-150 µm long, pharynx globular, no prepharynx. Esophagus opens into two long, unbranched caecae, which extend posteriorly on either side of the body to approximately 75% body length.

Ovary small, spherical (88-162 µm in diameter) and situated just anterior to mid-body. Genital pore located just behind pharynx, before the branching of the two caecae. Vitellaria are located in two longitudinal bands, each located laterally to the corresponding caecum, and extend from the level of the ventral sucker posteriorly to just past mid-body. Eggs seen in the uterus measure 36-38 x 24-28 µm). Two roughly spherical testicles, one on either side of the ventral sucker, 93-151 µm in diameter.

Life cycle & mode of transmission – Unstudied. In other Dicrocoeliidae, adults occupy the bile ducts

of the definitive host. Gravid females release eggs, which travel with the bile to the intestine and are shed in feces. The eggs are eaten by snails, where they hatch & develop into cercariae, then leave the snail within secretions. The secretions are eaten by ants, in which they become metacercariae; the definitive host is infected by eating the ants (Bowman, 2003).

Diagnosis at necropsy – Richard (1965) noted that their study material derived from the "hepatic canals" of *Microcebus murinus.*

Diagnosis in fecal examination – No study has linked appearance of adult *Zonorchis microcebi* directly to egg output in feces. Based on other Dicrocoeliidae, one would expect to see eggs in the fecal stream. Dicrocoeliidae parasitic in African colobine monkeys are ellipsoid, operculated and golden-brown, measuring 45 x 24 µm (Gillespie *et al.*, 2005).

Hosts – *Zonorchis microcebi* has been documented only in the original description, from *Microcebus murinus* from Mahabo (Richard, 1965).

Hogg (2002) noted "*Fasciola*" eggs in fecal examinations of *Eulemur rubriventer*, and Raharivololona (2006) noted "trematode" eggs in fecal examinations of *Microcebus murinus*; these may represent *Zonorchis* or a related species.

3. Acanthocephala

Though there is a long history of documenting acanthocephalan parasites in captive lemurs, little is known about whether lemurs harbor acanthocephalans in the wild. Shipley (1905) noted *Prosthenorchis spirula* infection in captive *Eulemur coronatus* and *E. mongoz* in London. Brumpt and colleagues (1938, 1939) described infections of *P. elegans* and *P. spirula* in monkeys and lemurs (including the lemurs *E. fulvus*, *E. albifrons*, *E. macaco*, *E. mongoz*, *Lemur catta*, and *Cheirogaleus major*) in captivity in Paris, transmitted via cockroaches as an intermediate host. Subsequently, Dollfus (1938) revised the taxonomy of the genus *Prosthenorchis* (Oligocanthorhynchidae), lumping *P. elegans* into *P. spirula* and reporting the latter from additional lemurs: *E. albifrons* and *C. major*, also in captivity in Paris.

However, as noted by Dollfus (1938), *P. spirula* had only been recovered in nature from the Neotropics (where it parasitizes Cebidae, Callitrichidae, Procyonidae, Mustelidae, and Myrmecophagidae); all observed infections of Old World hosts (including lemurs) were in captivity. Thus, the question of whether *Prosthenorchis* infects wild lemurs remained open (though other acanthocephalan genera infect wild birds, reptiles, amphibians, fish, and tenrecs; Dollfus & Golvan, 1963; Golvan, 1965; Golvan & Brygoo, 1965).

More recently, Machado Filho (1950) reviewed the genus *Prosthenorchis* and split *P. spirula* as recognized by Dollfus into several species, including *P. lemuri* and *P. dollfusi*, which are listed as parasitic of *Eulemur fulvus*. The fact that this study found morphological differences between worms found in lemurs and those of other primates is suggestive that these may represent lemur parasites in the wild, but without recovering specimens directly from wild lemurs, the question is still open.

Finally, more recent fecal examinations have reported Acanthocephalan-like eggs from wild lemurs: *Microcebus murinus* (Schad *et al.*, 2005; Raharivololona, 2006) and *Propithecus diadema* (Irwin & Raharison, unpub. data). This suggests that acanthocephalans may parasitize wild lemurs, but there is not enough evidence to identify the eggs reported to *Prosthenorchis*; they may represent another genus. Finally, there remains a possibility that the lemurs in question ingested definitive hosts (e.g. small frogs) and are passing undigested eggs. Only recovery of adult worms at necropsy from a wild lemur will provide definitive proof that they are infected by acanthocephalans.

4. Protozoa

The endoparasitic Protozoa of wild lemurs, both enteric parasites and blood parasites, remain almost completely unstudied. The strong research efforts dedicated to cataloguing the intestinal helminths (especially in the 1950s and 1960s) were not repeated for Protozoa. However, given their ubiquity among other primates (Rothman & Bowman, 2003), they are likely to be present in lemurs. Faulkner *et al.* (2004) recorded "amoebic protozoan parasites similar to *Entamoeba coli*, *Endolimax* sp., and *Iodamoeba* sp. from fecal samples of *Eulemur* spp., *Varecia variegata*, and *Lemur catta* (the sample included both captive and wild animals). Loudon *et al.* (2006) identified "coccidia" in *L. catta* feces and Raharivololona *et al.* (2007) identified "coccidia" from *Cheirogaleus major*, *C. medius*, and *Microcebus murinus*. Several bacteria species have been isolated from fecal cultures (reviewed in Junge & Sauther, 2006), but it is difficult to know which are commensals and which are parasites.

Eight species of blood-parasitic Protozoa are currently recognized. Uilenberg and colleagues

Table 3. Parasite species described or named from adult material recovered from lemurs currently not considered to be parasites of lemurs in the wild.

Helminth species	Circumstances of discovery	References
Enterobius anthropopitheci	Probably either an infection acquired in captivity, or a misclassification of a *Lemuricola* species (which had not yet been described).	(Baylis & Daubney, 1922; Chabaud *et al.*, 1965)
Buckleyenterobius dentata	Synonym of *Lemuricola lemuris*.	(Sandosham, 1950; Chabaud *et al.*, 1965)
Subulura otolicni	Parasite of African *Galago* spp.; probably acquired in captivity.	(Chabaud & Petter, 1958; Chabaud *et al.*, 1965)
Subulura prosimiae	Probably *Primasubulura distans*; infection probably acquired in captivity.	(Baer, 1935; Chabaud *et al.*, 1965)
Mastophorus muris	Found in wild *Daubentonia madagascariensis* but normally parasitizes *Rattus rattus*; probably accidental cross-transmission.	(Chabaud *et al.*, 1964, 1965)
Rictularia alphi	Discovered in a captive *Cheirogaleus* in Paris, never discovered in Madagascar; probably an infection acquired in captivity.	(Chabaud & Petter, 1958; Chabaud *et al.*, 1965)
Oxyspirura conjunctivalis	Found in *Microcebus* and *Loris tardigradus* in captivity in Berlin; never discovered in Madagascar.	(Baer, 1935; Chabaud *et al.*, 1965)
Trichuris trichiura	Trichurids found in lemurs have historically been assigned to this species, but there exists a species specific to lemurs (*Trichuris lemuris*) and no evidence of more than one species in lemurs.	(Chabaud *et al.*, 1965)

(1970, 1972) named two new species of Babesiidae (Sporozoa), *Babesia cheirogalei* from *Cheirogaleus major* held in captivity in Antananarivo and *B. propitheci* from a visibly ill wild *Propithecus coquereli* at Ampijoroa. These species are likely transmitted by an arthropod vector such as a tick, but the vector was not identified. Garnham & Uilenberg (1975) reviewed the *Plasmodium* reported from lemurs in 1975, and distinguished two species from microscopic analysis of infected erythrocytes. *Plasmodium girardi* Bück, Courdurier & Quesnel, 1952 has been described from *Eulemur rufus*, *E. macaco*, *E. fulvus*, and *E. mongoz* and *P. foleyi* Bück, Courdurier & Quesnel, 1952 has been described from *E. rufus*, *E. collaris*, and *E. fulvus*, though this species may in fact be a *Hepatocystis* (Cogswell, 2000). *Plasmodium lemuris* Huff & Hoogstraal, 1963 is considered synonymous with *P. foleyi*. More recently, four more species have been described: *P. coulangesi* Lepers, Rabetafika, Landau & Peters, 1989, and *P. bucki*, *P. percygarnhami*, and *P. uilenbergi* Landau, Lepers, Rabetafika, Baccam Peters & Coulanges, 1989.

Discussion

In summary, there have been 27 helminth species and 12 protozoan species described from lemurs (excluding species most likely to be infections acquired in captivity, species which have since been synonymized, and misclassifications; Tables 3, 4). Table 5 presents features of those helminth eggs expected to be found in feces.

The helminth and protozoan species described here likely represent only a fraction of the existing diversity, for four reasons. First, research efforts devoted to describing and classifying species were brief, largely confined to the 1950s and 1960s. Second, these research efforts were largely focused on helminths (especially nematodes); other taxa such as Trematoda, Acanthocephala, and Protozoa were largely ignored. Third, field research and collecting were largely restricted to a small number of reasonably accessible sites (e.g. Ampijoroa, Périnet, Nosy Be, Mahambo). The more recent parasitological studies from various new sites largely do not help document existing diversity, as they focus mainly on descriptions of eggs from fecal samples; eggs of closely-related helminth species (i.e. the products of adaptive radiations within Madagascar) often have similar appearance. Finally, other primate taxa whose parasites have been better sampled appear to harbor greater parasite diversity than has been documented for lemurs (e.g. 27 helminth species parasitic in 68 lemur species). For example, the great apes (Hominidae, excluding humans; n = 6 species) have at least 39 described parasitic helminth species, and the chimpanzee (*Pan troglodytes*) alone has 18 (Global Mammal Parasite Database, www.mammalparasites. org [Nunn & Altizer, 2005]).

Recent research is revealing the important effects that parasites can have on primate abundance, as well as shaping their behavior and social systems (Nunn & Altizer, 2006). Past decades of research have seen great advances in several diverse

Table 4. Eggs described from fecal examinations or blood smears whose determinations do not match helminth parasites of lemurs described to date.

Taxon detected / host	Diagnostic method / description of material	Likely to represent undescribed species?	Reference
Ascaris sp. / *Microcebus murinus*	Fecal examination: embryonated, rounded egg (width almost equal to length), with thick brown shell, 30-40 x 20-30 µm.	Possible – but hard to distinguish among *Ascaris* spp. based on egg morphology.	(Raharivololona, 2006; Raharivololona *et al.*, 2007)
"Ascarid" / *Microcebus murinus*	Fecal examination: embryonated, rounded egg (width almost equal to length), with thick brown shell, 65 x 45 µm.	Possible – but hard to distinguish among *Ascaris* spp. based on egg morphology; as noted by author, this may represent *A. lumbricoides*.	(Raharivololona, 2006; Raharivololona *et al.*, 2007)
Strongyloides sp. / *Cheirogaleus medius*, *Microcebus murinus*, *Indri indri*, *Propithecus diadema*, *P. verreauxi*, *Eulemur rufus*, *Lemur catta*, *Hapalemur griseus*, *Lepilemur edwardsi*	Fecal examination: symmetrical ovoid egg with thin wall, larvated, 60 x 35 µm, and rhabditiform larvae.	Yes – no Rhabditida yet described in lemurs.	(Faulkner *et al.*, 2004; Junge & Sauther, 2006; Raharivololona, 2006)
Oesophagostomum sp., *Ankylostoma* sp., *Chabertia* sp. / *Cheirogaleus medius*, *Microcebus murinus*	Fecal examination: symmetrical ovoid egg with thin wall, 65 x 35 µm.	No – hard to distinguish among Strongyles based on egg morphology; named genera not yet described in Madagascar. Specimens may represent *Lemurostrongylus*, and are of similar size.	(Raharivololona, 2006)
Capillaria (= *Calodium*) sp. / *Microcebus murinus*	Fecal examination: lemon-shaped, thick-walled egg with bipolar plugs, 45 x 23 µm.	No - hard to distinguish among Trichuridae based on egg morphology. Specimens may represent *Trichuris*, and are of similar size. Additionally, *Calodium* eggs would not be expected in feces unless an animal consumes the liver of a definitive host.	(Raharivololona, 2006; Raharivololona *et al.*, 2007)
Enterobius sp., *Heterakis* sp., *Syphacia* sp. / *Cheirogaleus medius*, *Microcebus murinus*	Fecal examination: asymmetrical bean-shaped egg with thin wall, 70-120 x 30-55 µm.	No – hard to distinguish among Oxyurids based on egg morphology. Specimens may represent *Lemuricola* or *Ingloxyuris*, and are of similar size.	(Raharivololona, 2006; Raharivololona *et al.*, 2007)
Hymenolepis sp. / *Cheirogaleus medius*, *Microcebus murinus*	Fecal examination: ovoid egg with circular space inside containing hexacanth embryo, 55-65 x 40-55 µm.	Yes – egg unlike either cestode described from lemurs.	(Raharivololona, 2006; Raharivololona *et al.*, 2007)
Cyclophyllidean cestode / *Cheirogaleus medius*, *Microcebus murinus*	Fecal examination: circular egg containing hexacanth embryo, (50 x 50 µm).	Yes – egg unlike either cestode described from lemurs.	(Raharivololona, 2006; Raharivololona *et al.*, 2007)
Coccidia (?*Eimeria* sp.) / *Cheirogaleus major*, *C. medius*, *Microcebus murinus*, *Eulemur rubriventer*	Fecal examination: no description given.	Yes – protozoan parasites of lemurs almost completely unstudied.	(Hogg, 2002; Raharivololona, 2006; Raharivololona *et al.*, 2007)
Nochtia sp. / *Eulemur albifrons*	Fecal examination: no description given.	Possible – but *Nochtia* is within Trichostrongyloidea and its eggs may be similar to *Pararhabdonema*.	(Junge & Sauther, 2006)
Anoplocephala sp., *Moniezia* sp. / *Propithecus edwardsi*	Fecal examination: no description given.	Possible – but eggs may be similar to other Anoplocephalidae (*Bertiella*).	(Hogg, 2002; Wright *et al.*, 2009)
Strongylus sp. / *Propithecus edwardsi*	Fecal examination: no description given.	No – eggs are likely indistinguishable from other Strongyles (e.g. *Lemurostrongylus*).	(Wright *et al.*, 2009)
Physocephalus sp. / *Propithecus edwardsi*	Fecal examination: no description given.	Possible – no Spirocercidae yet described from lemurs, but eggs may resemble other Spiruroidea (*Spirura diplocyphos*).	(Hogg, 2002; Wright *et al.*, 2009)
Fasciola sp. / *Eulemur rubriventer*	Fecal examination: no description given.	Possible – but eggs may resemble other Digenea (*Zonorchis*).	(Hogg, 2002)

Taxon detected / host	Diagnostic method / description of material	Likely to represent undescribed species?	Reference
Trichosomoides sp. / *Microcebus murinus*	Fecal examination: no description given.	Possible – but eggs may resemble other Trichuridae (*Trichuris lemuris*).	(Schad *et al.*, 2005)
Mansonella sp. / *Propithecus tattersalli*	Blood smears: microfilariae.	Unknown – microfilariae less diagnostic than adults, specimens may in fact represent one of the four species described in lemurs.	(Garell & Meyers, 1995)

Table 5. Key to identifying eggs of known helminth parasites of lemurs in fecal examinations.

Egg morphology	Corresponding helminth
Symmetrical ovoid egg with thin wall, 62 x 38 µm.	*Lemurostrongylus residuus*
Ovoid, thin-walled egg, 52-78 x 35-43 µm.	*Pararhabdonema longistriata*
Asymmetrical bean-shaped egg with thin wall, contents may be embryonated or undifferentiated, 57-105 x 22-48 µm.	*Lemuricola* (8 spp.) or *Ingloxyuris inglisi*
Asymmetrical bean-shaped egg with thick, striated wall and terminal operculum, contents may be embryonated or undifferentiated, 98-100 x 48-50 µm.	*Callistoura* (2 spp.)
Ovoid, embryonated eggs, 80 x 50 µm.	*Subulura baeri*
Embryonated, rounded egg (width almost equal to length), with thick brown shell; eggs of related species measure 50-75 x 35-60 µm.†	*Ascaris petiti*
Oval, smooth-shelled egg containing first-stage larva with a prominent cephalic hook, eggs of related species measure ~ 54-60 x 30-49 µm.†	*Spirura diplocyphos*
Oval, larvated egg with smooth thick-walled shells; eggs of related species measure 46 x 30 µm.†	*Rictularia lemuris*
Lemon-shaped, thick-walled egg with bipolar plugs, 55 x 26 µm.	*Trichuris lemuris*
Roughly circular, thick-walled egg, 35 – 40 µm in diameter. Shell composed of three concentric envelopes, innermost containing a single hexacanth embryo 13-18 µm in diameter with hooks 7-8 µm long, enclosed in a pear-shaped "piriform apparatus".	*Bertiella lemuriformis*
Packets of 5-12 eggs, 130-300 µm in diameter, with 6 – 12 ovoid eggs inside measuring 25-60 µm in diameter.	*Thysanotaenia lemuris*
Ellipsoid, operculated and golden-brown egg, measuring ~ 45 x 24 µm.†	*Zonorchis microcebi*
Ellipsoid eggs with thick 3-layered shell, containing an embryo (acanthor) with visible spines at one end, measuring 60-80 x 42-50 µm. May be brown.†	Acanthocephalan, possibly *Prosthenorchis* (2 spp.)

See corresponding text for citations.
† Eggs not described from Malagasy species, provisional description based on egg morphology of related species; see text for details.

aspects of primatology (e.g., behavior, socioecology, biogeography, taxonomy). In contrast, the parasites harbored by those primates remain relatively understudied, in terms of both the basic understanding of their diversity and classification, and their ecological relationships with, and effects on, their hosts (with the possible exception of parasites causing disease of public health importance, for which primates are used as human models). This imbalance may be because parasites are less visible to researchers in the field than other phenomena such as aggression, affiliation, sexual selection, and mate choice. Regardless, the result is that biologists studying lemurs may be lacking an important piece of the ecological framework for understanding their biology, behavior, and social organization. Further research is clearly needed in order to continue the discovery of new helminth and protozoan species parasitic of lemurs in the wild, as well as understanding their phylogenetic relationship,

host specificity, transmission ecology, and finally, their effects on population density.

Due to permit restrictions preventing killing lemurs to collect their parasites, it is much more difficult now to collect adult material of lemur parasites (especially helminths) than in the 1950s and 1960s. As a result, the most accessible and least intrusive way to study parasites in wild lemurs today is through observing the eggs shed in feces. Indeed, this is the method employed in most studies of lemur parasites over the past 20 years. However, the knowledge this yields is limited because determinations based on eggs are often limited to the genus or family level, while parasite adaptations and impact on the host can vary greatly even among closely related species. It is therefore important to collect adult worms whenever possible.

Researchers engaged in long-term lemur studies can harvest adult worms from opportunistically discovered cadavers, by dissecting the segments

of the digestive tract and washing the contents with water through a sieve (Gillespie, 2006). This yields direct observations of the adult helminths living in the animal's digestive tract. Additionally, rather than collecting feces directly into a fixative, they can be cultured in water, thereby inducing eggs found in feces to hatch (Gillespie, 2006). The larvae thus collected may be less diagnostic than adults, but might still yield more precise determinations than would be possible with eggs.

The knowledge yielded from an increase in these efforts at lemur research sites throughout Madagascar would be invaluable baseline data for monitoring changes in parasite prevalence and abundance (e.g. as anthropogenic disturbance increases), and potentially understanding complex changes in population ecology and behavior. This is especially important for the increasing number of lemur species threatened with extinction.

Conclusion

Despite recent advances in our understanding of lemur taxonomy, the study of the most basic natural history of lemur parasites remains poorly developed. In this paper, we summarize the current state of knowledge of lemur parasites (helminths and protozoans) and suggest that many more species remain to be discovered. Seizing opportunities to collect adult parasites from wild lemur populations will be key in filling in our knowledge of these parasites, and the data yielded by such efforts will be invaluable in future population monitoring, particularly in the face of increasing anthropogenic disturbance and ecological disequilibrium.

Acknowledgements

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