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A REVIEW OF DERMATROPIC SPECIES OF *LEISHMANIA* PRESENT IN PANAMA

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SUMMARY

A review of the 3 dermatropic species of *Leishmania* found in Panama and a brief discussion of their ecological relationships are presented. *L. hertigi* is a host-specific parasite of the porcupine *Coendou rothschildi*. It is found throughout the porcupine skin, but no gross skin alterations are manifest. The infection rate in adult porcupines is almost 100 % in all Panamanian localities, but young specimens are usually free of the infection. So far no vector of *L. hertigi* is known *L. mexicana* has been found in a single and isolated focus in eastern Panama. Three species of small rodents and a marsupial have been found naturally infected; the rice rat, *Oryzomys capito*, is considered to be the main reservoir host. *Lutzomyia olmeca*, a rodentophilic sandfly species, has been incriminated as the natural vector. Reservoir hosts are of terrestrial habits, and the incriminated vector is particularly active near the ground level. *Leishmania braziliensis* is the only leishmanial species isolated from humans in this country to date. Several feral mammals of the orders Edentata, Carnivora and Primates have been found with natural infections; dogs have also been found infected. The nature and course of infections vary in relation to the vertebrate hosts involved. In the principal reservoir host, the two-toed sloth *Choloepus hoffmanni*, the infection is a long-lasting one and does not produce any gross skin alterations. Five different sandfly species have been incriminated as vectors. *L. braziliensis* is closely associated with the tropical forest environment, and the prevalence of the infection is rapidly and adversely affected by deforestation.

RÉSUMÉ

Trois espèces leishmaniennes dermotropes ont été trouvées à Panama, ce sont : *Leishmania braziliensis, Leishmania mexicana* et *Leishmania hertigi*.

Ces espèces possèdent certains caractères propres en liaison avec leurs distributions géographiques, les Phlébotomes et les hôtes réservoirs, divers Mammifères arboricoles (Edentés, Carnivores, Primates). Le Chien aussi s'avère spontanément infesté par *L. braziliensis*. On rencontre *Leishmania mexicana* uniquement dans un foyer enzootique situé dans la région orientale de l'Isthme. Cette espèce fait partie d'un complexe écologique qui comprend *Lutzomyia olmeca* et de petits Mammifères terrestres, en particulier de petits Rongeurs. *Leishmania hertigi* est strictement liée à son seul hôte réservoir, le Porc-Epic (*Coendou rothschildi*). Jusqu'à présent, il n'a pas été possible de mettre en évidence un vecteur probable de cette espèce leishmanienne.

La nature et l'évolution de l'infection chez l'hôte naturel, sont nettement différentes pour chacune des trois espèces. On isole *Leishmania braziliensis* de la peau saine, des viscères et parfois du sang des Edentés. Chez les Carnivores sauvages, les Primates et le Chien, la localisation du parasite est limitée à la peau où il provoque des phénomènes de dépigmentation. Chez le Chien, les plages de dépigmentation sont parfois accompagnées de lésions ulcératives importantes au niveau des oreilles et de la truffe. La durée de l'infection est plus longue chez les Edentés et le Chien que chez les Carnivores sauvages et les Primates. *Leishmania mexicana* provoque des lésions cutanées au niveau de la queue de certains Rongeurs, mais jamais des viscères ou du sang. L'infection est chronique chez certains hôtes et seulement de courte durée chez d'autres. *Leishmania hertigi* essaime dans le tissu cutané sans altération apparente. On trouve parfois le parasite dans les viscères. Cette espèce provoque une infection chronique.

I. INTRODUCTION

The Republic of Panama is located in the neotropic region between 77°-83° longitude west and 7°-10° latitude north. It is a narrow country of about 75,500 square kilometers running in a general east-west direction. An important mountain range runs the length of the territory giving rise to 2 different hydrographic systems, the Pacific watershed to the south and the Caribbean (Atlantic) watershed to the north.

The geographic location of Panama and its particular physiography provide conditions which support a diversity of faunal and floral communities, with different ecological situations favorable to zoonoses, such as cutaneous leishmaniasis.

Human cutaneous leishmaniasis was first reported in this country shortly after the beginning of this century (DARLING, 1910). Thereafter, results of clinical and pathological studies were sporadic. Extensive investigations on the ecology of cutaneous leishmaniasis initiated at the Gorgas Memorial Laboratory in 1949 included studies on the taxonomy, geographic distribution, biology and habits of phlebotomine sandflies. These investigations were extended some years later to the reservoir hosts, natural transmission and other important aspects. Resulting from these continued efforts: (a) the phlebotomine sandflies of Panama, as well as their bionomics, are presently well known, (b) leishmanial infection was demonstrated in several species of sandflies, and (c) feral mammals with natural leishmanial infection were demonstrated for the first time in the New World.

The purpose of this paper is to review the most recent findings concerning dermatropic species of *Leishmania* present in Panama, emphasizing their principal ecological relationships.

II. MATERIALS

The present review is based mainly on investigations conducted by the authors and their associates during the past 9 years (April 1965 - March 1974).

1. Dermatropic species of *Leishmania*

Three distinct and easily differentiated species of *Leishmania* are presently known in Panama, *Leishmania hertigi* Herrer 1971, *Leishmania mexicana* Biagi 1952 and *Leishmania braziliensis* Vianna 1911.

The above three species of *Leishmania* show distinct differences in their geographic distribution, natural reservoir host affiliations and infection patterns in principal reservoir hosts.

Leishmania hertigi

This species of *Leishmania* was found in the tropical porcupine, *Coendou rothschildi*, in 1965 (HERRER *et al.*, 1966) and was subsequently described as a new species (HERRER, 1971). More recently, a wide geographic distribution of both the vertebrate host and its parasite in Panama has been reported (HERRER *et al.*, 1973).

As a total, 117 porcupines have been collected and studied. All of these animals were screened for leishmanial infections by skin biopsy and culture at least once. They were maintained alive in the laboratory from a few days up to 30 months. In most of the specimens kept alive for several months repeated skin biopsies were performed, and as many as 29 different skin samples for culturing were made from a single animal. Skin smears were made preferentially from porcupines whose skin cultures previously yielded a rapid and vigorous growth of promastigotes. Heart blood and viscera were cultured from 84 and 73 % of the animals, respectively. The age of the porcupines was arbitrarily estimated as "young", "juvenile", and "adult" on the basis of their weight, as follows:

(a) from 168 g to 900 g Young; (b) from 901 g to 1,500 g Juvenile; and (c) from 1,501 g and over Adult.

The lowest weight observed was 168 grams and the highest 2,951 grams. Also, 2 fetuses of infected adult females were processed for evidence of infection via transplacental transmission.

Nature and course of the infection

No gross skin alterations have ever been noted among the numerous infected porcupines thus far processed. In sections of the skin, small numbers of amastigotes are found in the upper dermis, where the only reaction observed is the presence of certain vacuoles in the cytoplasm of parasitized cells.

The parasites can be isolated easily in cultures from all the skin. However, the parasitism of the dorsal aspect of the animal is most intense (Table I). Although positive cultures are frequently obtained from liver and spleen, the parasite has never been found in stained smears of the viscera. Heart blood cultures usually yield negative results. The intensity of the parasitism is always very light. It is difficult to demonstrate parasites by skin smears even in cases whose cultures show vigorous and rapid growth. Parasites were demonstrated in stained smears of the dorsal skin of only 14 (45 %) of 31 animals whose cultures were positive for *Leishmania hertigi*. The nature and course of the infection does not appear to be altered during captivity of the porcupines.

Table I

Culture isolation of Leishmania hertigi *from different parts of the body of its vertebrate host,* Coendou rothschildi

Material cultured	Set of cultures*	Results	
		No. positive	% positive
Heart blood (99)**	111	1	0.9
Viscera (85)	260	98	37.7
Skin :			
Ventral aspect (84)	355	72	20.3
Dorsal aspect (117)	860	536	62.3

* Each set of cultures contained 5 or 6 tubes.
** Figures in parentheses indicate the number of animals involved in each case.

Geographic distribution

The presence of *Leishmania hertigi* has been demonstrated throughout the whole of Panama where its vertebrate host has been collected. This species of porcupine is present in all Panama lowlands except for the western extreme, where it is replaced by *Coendou mexicanus*. The latter species of porcupine has not been examined for leishmanial infections.

Host-specificity

The study of over 3,000 forest mammals in Panama during the last 9 years showed that *Leishmania hertigi* is found only in the porcupine, *Coendou rothschildi*. Also, under experimental conditions *Leishmania hertigi* behaves as a parasite of marked host-specificity. When inoculated intradermally into the nose of the golden hamster, the parasite remains at the site of inoculation for several months. Decreasing numbers of amastigotes were observed for some weeks by stained skin smears. The parasite was recovered in culture during shorter periods of time from several other species of rodents similarly inoculated with cultures of *Leishmania hertigi*.

Transmission

Nothing is known presently about the transmission of *Leishmania hertigi* in nature. Preliminary trials of experimental transmission using laboratory-reared sandflies *Lutzomyia sanguinaria*, fed on infected porcupines, showed that the insect may acquire the parasite from the porcupine skin. Nevertheless, only rare promastigotes were seen in the intestinal tract of this sandfly species for some days after the infective meal, and there was no indication of the establishment of a true infection (Herrer *et al.*, 1966).

Leishmania mexicana

Vertebrate hosts

This parasite has been found in 3 species of rodents, the rice rat *Oryzomys capito*, the spiny rat *Proechimys semispinosus*, the paca *Agouti paca*, and one marsupial, the brown murine opossum *Marmosa robinsoni*. Infection rates were significative only among the first 2 species of rodents, 14 (36 %) of 39 *Oryzomys capito* and 8 (4 %) of 202 *P. semispinosus*.

Nature and course of the infection

Leishmania mexicana behaves in *Oryzomys capito* as a well adapted parasite, both in natural and experimental infections. Although the infection produces certain skin lesions, most frequently on the tail, and lasts for long periods of time it apparently does not affect the health of the rat. The parasite appears restricted to the skin, and cultures from viscera consistently gave negative results even in specimens infected for long periods of time.

The spiny rat, *Proechimys semispinosus*, seems to be rather resistant to the infection with *Leishmania mexicana*. Laboratory-bred specimens experimentally inoculated with cultures, and several obtained infected in nature, proved to harbor the parasites for a few weeks only. This would suggest that this rodents species is probably an incidental reservoir host in Panama and plays only a minor role in maintaining the infection in nature.

Geographic distribution

So far *Leishmania mexicana* seems to be restricted to a single small enzootic focus in Sasardi, eastern Panama. Intensive field studies conducted during 1968 and 1969 helped to elucidate the principal species of forest mammals involved, the composition of phlebotomine sandfly population and the insular nature of this endemic focus. Other areas of eastern Panama were surveyed in subsequent years, with negative results. Also, we have yet to find *Leishmania mexicana* in central Panama where we have carried out intensive studies on natural leishmaniasis among feral mammals for several years (Herrer *et al.*, 1973). Our investigations in western Panama have been far less extensive than other areas of this country. We have encountered *Leishmania hertigi* and *Leishmania braziliensis* but not *Leishmania mexicana* in this region.

Incriminated insect vector

From more than 20 different sandfly species collected from traps and resting places, *Lutzomyia olmeca* clearly emerges as the principal potential vector of *Leishmania mexicana* in the enzootic focus of Sasardi. The complete dominance (99 %) of this sandfly species in traps baited with small rodents is particularly indicative.

Leishmania braziliensis

Vertebrate hosts

It is likely that most of the Panamanian forest mammals are susceptible to this parasite. Natural infections have been demonstrated in 7 different feral mammals of the orders Edentata, Carnivora, and Primates. Furthermore, *Leishmania braziliensis* it the only species of *Leishmania* isolated from humans in Panama to date.

Nature and course of the infection

Clinical manifestations vary in relation to the vertebrate host involved. In edentates the infection is completely cryptic and lasts for long periods of time. Also, the parasite is frequently isolated in culture from viscera as well as from the skin. In forest carnivores the only evidence of infection is skin depigmentation. However, in dogs such depigmentations frequently give rise to large and destructive skin lesions on the nose and ears. The duration of the infection also varies according to the species of carnivore involved, but in all of them the parasite is restricted to the skin.

Geographic distribution

This species of *Leishmania* is widely distributed throughout the forested areas of Panama up to about 600 meters above sea level. When man's activities bring him into contact with the sylvatic environment, he is usually unaware that he has encroached upon an endemic focus of *Leishmania braziliensis* until the characteristic skin lesions appear on the unclothed areas of his body.

Transmission

On the basis of phlebotomine host feeding records, relative abundance and natural or experimental infections, the following sandfly species have been incriminated as potential vectors of *L. braziliensis* in Panama (CHRISTENSEN and HERRER, 1973) : *Lutzomyia trapidoi, Lutzomyia gomezi, Lutzomyia sanguinaria, Lutzomyia ylephilator,* and *Lutzomyia panamensis*. All are fairly common species in most parts of the Panamanian forest and known to feed on several feral reservoirs as well as man.

2. Some ecological considerations

Leishmania hertigi

The dissemination of this parasite throughout the porcupine skin is remarkable. The complete absence of any gross indication of the infection suggests a well balanced host-parasite relationship. Such a relationship, which appears to be commensal rather than parasitic, could be responsible for the very high infection rates observed among adult porcupines throughout Panama. This supposition is supported by the long-lasting nature of the infection that we have observed in specimens maintained in captivity, as well as by the incidence of the infection in older porcupines (Table II).

Table II

Infection rate of Leishmania hertigi *in relation to the estimated age of its vertebrate host,* Coendou rothschildi

Estimated age	Total	No. studied	
		Found infected	Infection rate
Fetus*	2	0	---
Young	12	3	25.0 %
Juvenile	18	15	83.3 %
Adult	47	47	100.0 %

* Both fetuses studied were already covered by hair at the time their mothers were killed and the autopsies performed.

Negative results obtained in 2 fetuses, together with the low infection rate found in young specimens (Table II), indicate that porcupines acquire the infection soon after their birth, and that it is not transplacentally transmitted. Literature concerning the transmission of Leishmaniae dictates that prime consideration be given to phlebotomine sandflies as the most plausible vector of *Leishmania hertigi*. THATCHER (1966) found that porcupines were highly attractive to *Lutzomyia panamensis,* an incriminated vector of *Leishmania braziliensis* in Panama. On the other hand, 13 different ectoparasites have been reported from this species of porcupine (WENZEL *et al.*, 1966). Among them there are 3 ticks and 9 mites, which also deserve consideration in the search for the natural vector of *Leishmania hertigi.*

Leishmania mexicana

The restriction of *Leishmania mexicana* to the small and isolated enzootic focus in eastern Panama may be explained on the basis of the abundance of the sandfly vector in this area in comparison with other Panamanian regions. Although *Leishmania mexicana* has been shown to develop experimentally in several different sandflies, its transmission in the forests of the New World has been attributed thus far only to *Lutzomyia olmeca* and *Lutzomyia flaviscutellata,* two closely related

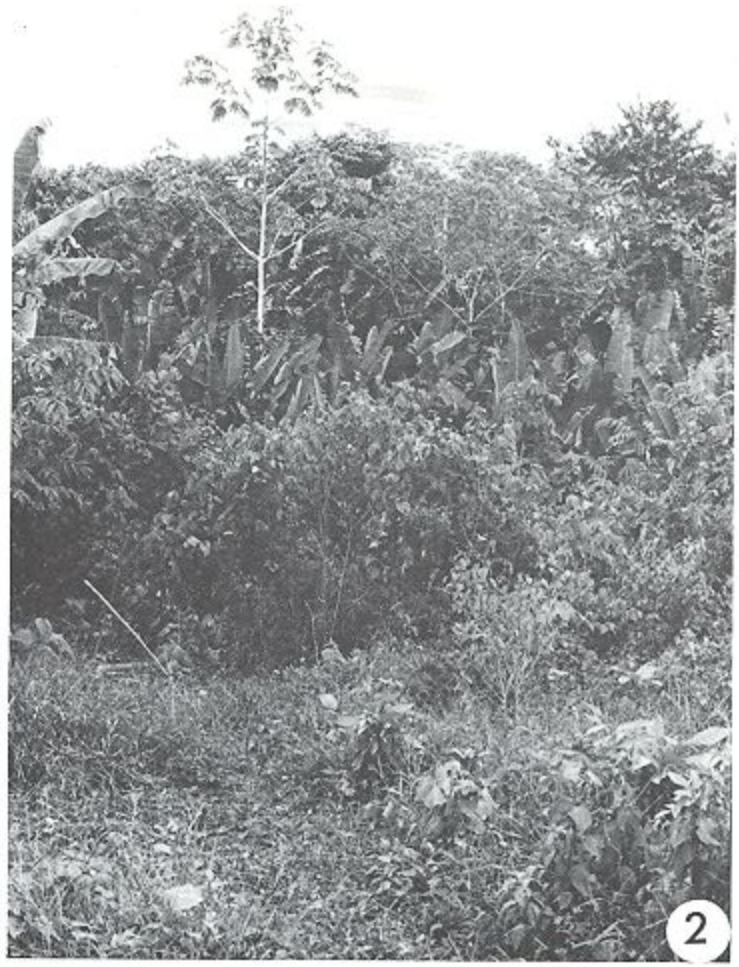

PLATE I

FIG. 1. — Type of treehole where the tropical porcupine, *Coendou rothschildi*, is found. Arrows show a large hollow at the base of the tree which connects with an opening at the 2.5 m level.

FIG. 2. — Part of the study area in Sasardi, eastern Panama, where an enzootic focus of *Leishmania mexicana* was discovered in September 1968. Different stages of plant succession in this secondary forest can be observed. Most of the infected rice rats *Oryzomys capito* and spiny rats *Proechimys semispinosus* were collected in the area covered by herbaceous plants.

PLATE II

FIG. 3. — The initial stages in the establishment of a small community in an area of primary forest. Trees are cut down for some distance to provide a clearing around human dwellings, depending upon the number of settlers and their economical status. In this situation, *L. braziliensis* remains endemic in the nearby forest and man and dogs are frequently infected. FIG. 4. — When settlers establish larger communities, or if the land is to be used for cattle grazing, a greater area is cleared and the trees are burned. In this situation the environment is unsuitable for hosts and vectors, and *L. braziliensis* disappears.

species. Intensive collection of sandflies in Panama during recent years has shown that *Lutzomyia olmeca* is present throughout most of the country as a relatively uncommon species except in certain areas such as Sasardi, where it represented the third most abundant species. Results of comparative collections made with traps baited with small rodents in Sasardi and 2 localities of central Panama illustrate this statement. *Lutzomyia olmeca* comprised 99.1 % of the sandflies from animal-baited traps in Sasardi, in comparison to 1.8 % and 2.4 % in the 2 localities of central Panama (CHRISTENSEN *et al.*, 1972; CHRISTENSEN and HERRER, 1973).

The rice rat *Oryzomys capito*, the principal reservoir host of *Leishmania mexicana* in Sasardi, is found also in other areas of Panama. The same is true for the other two rodent species, the spiny rat *Proechimys semispinosus* and the paca *Agouti paca*, as well as the marsupial *Marmosa robinsoni*, found infected with *Leishmania mexicana* in Sasardi (HERRER *et al.*, 1971). All these mammals are present in central Panama, and many have been processed in the search for leishmanial infections during recent years, with negative results (HERRER *et al.*, 1973).

There are signs which seem to indicate a recent establishment of the enzootic focus of *Leishmania mexicana* in Sasardi. Infected mammals were collected exclusively in an abandoned agricultural area previously planted with corn and rice (TELFORD *et al.*, 1972). At the time of our first visit (September, 1968) natural vegetation was reverting to secondary forest (Fig. 2) in the area where infected animals were collected. Small terrestrial rodents, mainly *Proechimys semispinosus* and *Oryzomys capito*, were common in this area in comparison with adjacent agricultural (a coconut plantation) and primary forest communities. The intensive trapping conducted between September, 1968 and June, 1969 reduced markedly the population of *Oryzomys capito* to the point that a single specimen was captured in June, 1969 (TELFORD *et al.*, 1972).

It seems very likely that the abundance of food from the corn and rice plantations, together with the variety of habitats provided by the subsequent development of a secondary forest in the study area, enhanced conditions for increased populations of small terrestrial rodents in a relatively short period of time. The rapid decrease in the number of *Oryzomys capito* with the intensive trapping might indicate that this rat was not well established by the time of our visits.

Leishmania mexicana was found in Sasardi only in mammals collected in traps set at ground level. This seems to be the result of ecological associations between the reservoir hosts and the incriminated insect vector. *Oryzomys capito*, the principal reservoir hosts of *Leishmania mexicana* in Sasardi, is a rodent with strict terrestrial habits. The near ground flight activity of *Lutzomyia olmeca* observed in Sasardi (CHRISTENSEN *et al.*, 1972), has been observed in British Honduras as well (DISNEY, 1968; WILLIAMS, 1970).

Leishmania braziliensis

Active transmission occurs from ground level to the upper canopy of primary forest because the diversity of vectors and reservoir hosts include terrestrial, arboreal and scansorial species. The zoonosis may also persist in secondary forests of sufficient maturity to provide the necessary microhabitats and microclimatic conditions to sustain vector and host populations. Man and dogs are only incidental hosts and become involved in the transmission cycle only if their activities bring them into contact with sylvatic foci.

As a result of ever increasing population pressures, deforestation is becoming more and more a common practice in Panama, as families and small groups of farmers (campesinos) establish new communities in previously untouched forested areas. The slash and burn agricultural practices of these people bring them into intimate contact with endemic foci of *Leishmania braziliensis*, and outbreaks of epidemic proportions ensue. It is not clear if man and dogs actually participate in the cycle of the parasite under these conditions. Dogs have been shown to be fairly attractive to at least one potential vector species (CHRISTENSEN and HERRER, 1973). It is possible that these animals may provide an ancillary source of infection for sandflies within the settlements themselves. *Leishmania braziliensis* gives rise to long lasting infections in these animals.

The long term result of the accelerated deforestation is the gradual extinction of leishmaniasis from these areas in which vector-host relationships become disrupted.

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DISCUSSION

P.C.C. Garnham : The title of the paper was "Dermatropic species". You stated that *Leishmania hertigi* was often found in the viscera. Can you reconcile the use of this term ? When Dr. LEWIS and I were working in Belize many years ago, we thougt that the kinkajou might be a reservoir of *L. mexicana*, but the only specimen we caught was negative.

A. Herrer : It is necessary first to known what we understand by visceralization. To me, visceralization is the *establishment* of the infection in viscera. So far, it has not been possible to demonstrate the parasite in the viscera by smear or sections, so it is possible that some of the very few infected cells which circulate with the blood are picked up with viscera sample used for culture.

D.J. Lewis : Is it possible that, when the forest is destroyed, *Lutzomyia longipalpis* will appear and enable *Leishmania chagasi* to flourish ?

A. Herrer : Up to the present time very few specimens of these sandflies have been found in Panama, and all in areas devoid of primary forest.

A. Nadim : You mentioned you do not know the vector of *L. hertigi*. What would be your method to determine the vector of this *Leishmania ?*

A. Herrer : We don't know yet.

R. Lainson : I was particulary interested to hear of Dr. HERRER's isolation on the *L. mexicana* subspecies from *Oryzomys* in Panama, and that he felt that *Oryzomys capito* was the principal host with the lesions appearing on the tail; also that he felt that *Proechimys* was not a good host because he did not see similar tail lesions in this animal. In Brazil, we at first thought that *Oryzomys capito* was the major host of *L. mexicana amazonensis*, again with prominent lesions on the tail. More recently, however, we have found that *Proechimys guyanensis* is a much more important host in the Amazon Region, 26 infections were found in 166 of these rodents examined (15.7 %) along the new Transamazon Highway. In 21 of these, the infection was generalized, in perfectly normal looking skin, with no ulceration. We feel that animals with this well balanced host-parasite relationship are more likely to represent the natural host of the *Leishmania* in question, just as Dr. HERRER has described in the case of *L. hertigi* and the porcupine, *Coendou*.

V.M. Safyanova : I have two questions :

— What is the behaviour of *L. hertigi* in golden hamsters ? Is it pathogenic for hamster ?

— How do you explore the host-parasite relationship in the case of *L. hertigi* and porcupines ? Is it a specific biochemical adaptation or, may be, the result of food preference of the vector ?

A. Herrer : We don't know, but I suppose it is due to both the vertebrate host and the parasite.

W. Peters : Can we now call your "*braziliensis*" either *L.b. panamensis* or *L. panamensis*, now that we have clear criteria for the nomenclature ?

A. Herrer : We called it just *L. braziliensis*.