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Reptiles and their Importance in the Epidemiology of Leishmaniasis

E. M. BELOVA[1]

Promastigote flagellates have been isolated from various species of lizard and from some other reptiles. It is known that sandflies readily feed upon lizards and it has been thought that reptiles could be a reservoir for mammalian leishmaniasis. A feature of reptilian infections is the extreme scarcity of parasites in blood smears and in tissue impression smears but isolations may readily be made in culture media. The intradermal inoculation of promastigote cultures from lizards into mammals and man induces a positive leishmanial response and gives rise to long-lasting dermal knots from which living parasites can be recovered for periods of several months.

Associations between promastigotes and lizards in parts of the USSR, particularly in the Turkmenian SSR, and experimental work in the USSR on the transmission of promastigote strains to a variety of mammals, including gerbils, mice, monkeys, and man, are reviewed. The author accepts the generally held view that although promastigote flagellates of reptiles are important in an evolutionary context, having probably given rise to the mammalian leishmanias, present-day strains must be considered nonpathogenic for mammals.

Along with known reservoirs of leishmanias in mammals there is also a group of reptiles, mainly lizards, that harbours *Leishmania* infections. The part they play in spreading leishmaniasis is not yet clear. Published data on the role of the cold-blooded animals in leishmaniasis epidemiology are few and rather contradictory and are based on the finding of promastigotes in some species of reptile and on the studies of the isolated parasites in artificial nutrient media.

One of the first reports of reptiles being carriers of promastigotes was made by Sergent, Lemaire & Senevet (Jakimov, 1915), who studied the gecko, *Tarentola mauritanica*, in Algeria. Blood from geckos was cultured on N.N.N. nutrient medium and flagellates were obtained in 15.7% of the cultures. These flagellates were morphologically similar to the promastigote stage of *Leishmania tropica*. On these grounds, it was assumed that geckos were possibly important as natural reservoirs of cutaneous leishmaniasis.

The first report of spontaneous infection of geckos with " leishmaniasis " in the USSR was made by Šahsuvarli (1934). He did not attach great importance to his finding and made only a brief remark about the discovery of an infected gecko in the Turkmenian SSR. Two years later, Zmeyev (1936) reported the discovery of promastigotes in 1 out of 7 tissue smears taken from *Eremias lineolata* Nik. in Tajikistan. In studies of 68 lizards from the Bakharden district in Turkmenia, Hodukin & Sofiev (1940) found promastigotes in 1 of 20 specimens of *Phrynocephalus mystaceus* Pall., in 1 of 18 *Agama sanguinolenta* Pall., and in 2 of 15 *Phrynocephalus heliscopus* Pall. In all cases, promastigotes were discovered only when isolated in culture. Neither leishmanias nor promastigotes were found in blood smears or in viscera impression smears.

Latyšev & Pozyvaj (1937) and Latyšev (1949) investigated the lack of agreement between the results from microscopy and from culture techniques, using both methods to study the infection in more than 200 *Gymnodactylus caspius* Eich. from different parts of the Murgab River valley in Turkmenia. Promastigotes were found in cultures of tissues isolated from many specimens but they were not found microscopically in the blood or organs. Popov (1941) reported finding promastigotes in blood smears from 3 Caspian geckos, which were among many lizards studied by him in Azerbaidzhan.

[1] Turkmenian Institute of Epidemiology and Hygiene, Ashkhabad, Turkmenian SSR.

Table 1. Species composition of lizards examined for leptomonad infection in the Turkmenian SSR

Family	Species	Number of specimens of each	
		species	family
Agamidae	*Phrynocephalus interscapularis* L.	926	1 771
	Agama sanguinolenta Pallas	683	
	Phrynocephalus mystaceus Pallas	99	
	Agama caucasica Eich.	39	
	Phrynocephalus raddei raddei B.	20	
	Phrynocephalus helioscopus Pallas	4	
Lacertidae	*Eremias velox* Pallas	354	1 005
	E. intermedia Strauch	277	
	E. guttalata guttalata Licht.	169	
	E. lineolata Nik.	113	
	E. grammica Licht.	88	
	E. scripta scripta Strauch	4	
Gekkonidae	*Gymnodactylus caspius* Eich.	907	1 015
	Teratascincus scincus Schlegel	101	
	Gymnodactylus russowi Strauch	3	
	Crossobamon eversamani Wieg.	4	
Anguidae	*Opisaurus apodus* Pallas	13	20
	Mabuya aurata L.	7	
Varanidae	*Varanus griseus* Daudin	4	4
Scinciidae	*Eumeces taeniolatus* B.	1	3
	E. schneideri princeps Daudin	2	

In Turkmenia in 1951–52 Andruško & Markov (1955) found promastigotes in blood smears of *Phrynocephalus interscapularis* and *Eremias intermedia* in Molla Kara and of *Eremias intermedia* and *Eremias grammica* at the Akhcha-Kuyma station on the Ashkhabad railway.

A large survey of leishmanial infection in reptiles was carried out by the author in the Turkmenian SSR between 1963 and 1966. During the 3 years, a total of 3 818 lizards and 9 snakes were studied in 16 different areas. The lizards represented 6 families and 21 species (Table 1) and 11 species were found to be carriers of promastigotes; 6 species were known previously as carriers of promastigotes in the Turkmenian SSR and 5 species were discovered for the first time to be carriers. The infection was confirmed in *Gymnodactylus caspius*, *Agama sanguinolenta*, *Phrynocephalus interscapularis*, *Phrynocephalus mystaceus*, *Eremias intermedia* and *Eremias grammica*. *Teratascinus scincus*, *Phrynocephalus raddei raddei*, *Eremias velox*, *Eremias lineolata* and *Eremias guttulata guttulata* were also found to be infected, 4 out of these 5 species (with the exception of *Eremias lineolata*) being registered as promastigote carriers for the first time, not only for Turkmenia but anywhere.

Table 2. Leptomonad findings in lizards at different places in the Turkmenian SSR, 1963–66

Places in which infected lizards were found	Species of lizard infected	No. of specimens examined	No. of lizards with promastigotes
Ashkabad	*Phrynocephalus interscapularis L.*	520	5
	Agama sanguinolenta	351	20
	Eremias intermedia	170	1
	Eremias velox	99	1
	Eremias lineolata	90	4
	Gymnodactylus caspius	47	2
	Phrynocephalus mystaceus	63	1
Imam-Baba	*Agama sanguinolenta*	125	18
	Eremias intermedia	99	2
	Eremias velox	84	7
	Eremias grammica	47	2
	Eremias lineolata	20	1
	Gymnodactylus caspius	13	5
Serakhs	*Gymnodactylus caspius*	708	123
	Eremias guttulata guttulata	159	3
	Eremias velox	73	2
	Agama sanguinolenta	66	3
Kara-Kala	*Gymnodactylus caspius*	122	9
	Eremias velox	92	1
Mary	*Phrynocephalus raddei raddei*	19	2
Sarykamys Valley (Cukurlyk sector)	*Teratascincus scincus*	77	1
	Phrynocephalus interscapularis	73	2
Senekli Baharden Rayon	*Phrynocephalus interscapularis*	212	6
Anau	*Phrynocephalus interscapularis*	66	2

Infected lizards were found in 8 areas of Turkmenia—namely, Ashkhabad, Imam-baba, Serakhs, Kara-Kala, Mary, Chukurlyk village in the Sarykamish depression and at the Senekli well in the Bakharden district. Usually at each locality there was not one but several species of infected lizard (Table 2). The highest rate of infection was usually found in *Gymnodactylus caspius* (20–30%) and *Agama sanguinolenta* (up to 14.5%).

Infections were revealed almost exclusively by isolating blood from heart or liver blood or pieces of tissue in N.N.N. medium. Slants of blood-agar supplemented by an enrichment liquid containing antibiotics were also used. In tissue smears and impressions, parasites were revealed in the promastigote form in 4 cases only (2 *Phrynocephalus interscapularis* and 2 *Agama sanguinolenta*). It can be concluded that the technique of culture isolation is the most reliable for revealing promastigotes in infected lizards. The agreement of results from simultaneous studies of heart blood, liver blood and tissue samples from the same specimens indicates that any of these will provide reliable information on leishmanial infections in lizards.

It has been found that promastigotes are present in lizards in Turkmenia at all seasons, and the author believes that lizards may remain infected for life. This supposition is based first of all on the finding of infected lizards under natural conditions in winter and early spring, before the first generation of sandflies has appeared. In 1964, studies of geckos in Serakhs were undertaken early in April before sandflies emerged. Out of 56 geckos, 11 (20%) were found to have promastigotes and that proportion was only 6% lower than the infection rate the previous year when the epidemic season was at its height. Infection of geckos caught in spring might take place in autumn or earlier; thus the minimum duration of parasite survival in geckos, as shown by these studies, is about 5–6 months.

The long-term survival of promastigotes in reptiles has been confirmed also by observations on naturally infected lizards in the laboratory. Some specimens of *Gymnodactylus caspius* and *Agama sanguinolenta*, after the natural infection by promastigotes had been confirmed, were kept in the laboratory for repeated investigation after 1½–2 months. All of them gave positive results.

In order to exclude the possibility of transovarian transmission of promastigotes in reptiles, 3 young *Gymnodactylus caspius* bred in the laboratory from the eggs of females spontaneously infected by promastigotes were studied for the presence of infections. The results of the studies allowed the possibility of parasite transmission to progeny to be excluded. The infection seems to arise invariably from sandfly bites.

The ability of sandflies to feed on reptile blood has been reported a number of times. Petriščeva (1949) has repeatedly observed *Phlebotomus papatasi* females and sandflies of the genus *Sergentomyia* sucking blood from geckos. Minter & Wijers (1963) stated that *S. clydei* and *S. schwetzi* feed mainly on the blood of reptiles. Raynal (1954) reported that in France *S. minuta* were feeding only on snakes and lizards and Simič (1930) mentioned the bloodsucking activity of sandflies on cold-blooded animals in Yugoslavia. The present author carried out experiments between 1965 and 1966 on sandflies of three species (*P. papatasi*, *P. caucasicus*, and *S. arpaklensis*), allowing them to feed on *Agama sanguinolenta* and *Gymnodactylus caspius*. All the three species of sandfly proved able to bite these lizards.

Andruško & Markov (1955) gave attention to the fact that the promastigotes were more easily found in preparations from young lizards. They concluded that young lizards are more susceptible to promastigotes and believe the reason to be the thin skin and low resistance of young lizards. This conclusion has not been confirmed by the author's own observations; nearly the same rate of infection has been seen in all age groups. Infection may occur more easily and quickly in young lizards but feeding experiments have shown that infection of adult lizards is not excluded.

To the extent that reptiles, particularly lizards, are in close association with sandflies and wild rodents under natural conditions, it is supposed that leishmanias are transmitted to them from warm-blooded animals by sandflies. For a clear understanding of the epidemiological importance of reptiles it is necessary to study the nature of reptile promastigotes and their relationships to pathogenic mammalian leishmanias. At the present time there is no uniform opinion on the role of reptile promastigotes in human and animal pathology.

Of the natural infection of *Gymnodactylus caspius* by promastigotes in Turkmenia Latyšev (1940) wrote: " these reptiles have occupied a stable place in the list of animals suspected of being carriers of cutaneous leishmaniasis ". However, when negative results were obtained from 174 geckos in the Takhta-Bazar and Serakhs districts of the Turkmenian SSR, Latyšev & Pozyvaj (1937) were doubtful about the importance of reptiles in the epidemiology of cutaneous leishmaniasis. Krjukova (1941), after experiments on animals and human volunteer subjects, came to the conclusion that promastigotes of geckos were specific reptilian parasites and had nothing to do with the appearance of leishmaniasis in warm-blooded animals. Hodukin & Sofiev (1940), after studying strains of leishmanias from three species of lizards in Central Asia (*Agama sanguinolenta*, *Phrynocephalus helioscopus* and *Phrynocephalus mystaceus*) stated with confidence that lizard promastigotes are not pathogenic for mammals and man. Šurenkova (1947) also held the same opinion and even suggested that the reptile promastigotes belong to an independent genus.

Koževnikov et al. (1950) held a somewhat different opinion on this point. They observed that intracutaneous inoculations of promastigotes from geckos in persons who had recovered from cutaneous leishmaniasis produced allergic reactions at the site of the inoculation, and they considered this to be evidence of antigenic affinity between the human and the reptilian parasites. They also believed that reptilian strains of promastigotes might be used for the artificial immunization of man against cutaneous leishmaniasis.

One way to clarify the nature of reptilian promastigotes and their relationship to leishmanias of man and other warm-blooded animals is to investigate experimentally the susceptibility of lizards to promastigote cultures of different origin. Kandelaki (1939) reported the successful inoculation of 7 *Agama caucasica* in the Georgian SSR with strains of visceral leishmaniasis. Hodukin & Sofiyev (1940) tried to inoculate *Gymnodactylus caspius* with strains of *Leishmania* isolated from lizards and a dog; the results were negative in both cases. In recent years, the present author has carried out inoculation experiments on 14 species of lizard with different promastigote cultures. Only lizards that were definitely not carriers of promastigotes were used in the experiments. The inocula used were as follows: cultures of the causative agent of zoonotic cutaneous leishmaniasis from human patients and from gerbils, cultures of the causative agent of visceral leishmaniasis, and promastigotes of sandfly and reptilian origin.

The strains of visceral leishmaniasis were isolated from a sick child and a spontaneously infected dog in Turkmenia. Sandfly strains were isolated from *Phlebotomus caucasicus* in foci of visceral leishmaniasis in the Takhta-Bazar district of Turkmenia. The isolation of *Leishmania tropica* cultures and reptilian promastigotes was carried out by the author in Turkmenia; promastigote strains from 5 species of lizard (*Agama sanguinolenta, Gymnodactylus caspius, Phrynocephalus interscapularis, Eremius intermedia, Eremias velox*) were tested. All the strains of reptilian origin, except one from *Phrynocephalus interscapularis*, were morphologically identical with the other strains. Strains of promastigotes of a completely different type, pear-shaped or even rounded, which were obtained from *Phrynocephalus interscapularis* together with promastigotes of the usual shape, were also isolated in some other places. One such strain has been included in the total number of cultures of reptilian origin that was tested.

Inoculation was mostly carried out subcutaneously on the inner side of the hind foot but in some cases inoculation was intraperitoneal. The susceptibility of lizards to different cultures was assessed by the results of trials at various times after the beginning of the experiment.

The studies showed that lizards had a very low susceptibility to all cultures except that containing the rounded promastigotes, some species of lizards being rather susceptible to this culture. In the experiments with other strains, only isolated positive results were obtained (Table 3). Positive results were registered from inoculations with a visceral leishmaniasis strain in *Agama sanguinolenta, Gymnodactylus caspius, Eremias intermedia* and *Phrynocephalus interscapularis*; from inoculations with reptilian strains positive results occurred in *Agama sanguinolenta, Gymnodactylus caspius, Eremias lineolata, Eremias intermedia* and *Eremias velox*; inoculations with sandfly strains gave positive results only in *Gymnodactylus caspius*. The rare cases of experimental infection of lizards by leishmanias from warm-blooded animals can be considered as proof of a remote genetic affinity between reptilian promastigotes and leishmanias of man and warm-blooded animals. The affinity of reptilian promastigotes to pathogenic leishmanias has also been confirmed by the results of experimental studies of reptilian cultures inoculated in human subjects and warm-blooded animals. Yung & Herting (Popov, 1941) found that gecko flagellar parasites caused changes in hamsters that were characteristic of American kala azar. In recent years, Manson-Bahr & Heisch (1961) tested a promastigote culture of *Leishmania adleri* isolated from a lizard (*Latastia* sp.) in human volunteer subjects and recorded the appearance of skin knots reminiscent of the papules caused by the inoculation of *Leishmania donovani*. The specificity of such knots was confirmed by finding parasites in smears and by the isolation of the living promastigote culture on N.N.N. medium.

During 1963–66 the present author carried out inoculation experiments in white mice, golden hamsters, and red-tailed gerbils, using 7 strains of reptilian promastigotes obtained from *Gymnodactylus caspius, Agama sanguinolenta, Phrynocephalus interscapularis, Eremias intermedia, Eremias velox*, and *Eremias guttulata guttulata*. Subcutaneous, intracutaneous, and intraperitoneal inoculations were made and the experimental animals were observed for 2–3½ months. The results were negative in all cases. Negative results had also been obtained by Hodukin & Sofiev (1940), who inoculated cultures from 3 species of lizard from Central Asia into human volunteer subjects, monkeys, hamsters, and

Table 3. Data on the infection of lizards with various promastigote cultures

Culture	Number of infected lizards														
	Total	*A. sanguinolenta*	*G. caspius*	*P. interscapularis*	*Eremias intermedia*	*Eremias velox*	*Eremias lineolata*	*Phrynosephalus mystaceus*	*Agama caucasica*	*Tetrascincus scincus*	*Eremias guttulata*	*Eremias grammica*	*Mabuya aurata*	*Eumeces schneideri*	*Varanus griseus*
L. tropica	321	51	92	67	38	37	2	3	21	3	1	4	1	—	1
L. donovani	204	53	45	29	24	20	20	4	4	4	—	—	1	—	—
L. canis	51	10	—	40	1	—	—	—	—	—	—	—	—	—	—
from *Phlebotamus caucasicus*	129	27	36	25	4	—	2	27	—	—	7	—	—	1	—
from *Gymnodactylus caspius*	148	49	43	19	14	6	10	1	1	5	—	—	—	—	—
from *Phrynocephalus interscapularis*	84	23	12	45	—	—	—	—	—	—	—	4	—	—	—
from *Agama sanguinolente*	53	19	3	—	17	—	13	—	1	—	—	—	—	—	—
from *Eremias velox*	8	8	—	—	—	—	—	—	—	—	—	—	—	—	—
from *Eremias intermedia*	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—

white mice, and also by Krjukova (1941) who studied the pathogenicity of a strain from *Gymnodactylus caspius* in gerbils, mice, and human volunteer subjects.

The data from histological studies made by S. E. Gleyberman (unpublished data) on the skin of gerbils and mice that had been inoculated with a strain of *Leishmania* from *Gymnodactylus caspius* are of great interest. The experimental gerbils were killed at different times after the inoculation and the skin of gerbils killed 2–4 hours after inoculation showed loosening of the dermis, oedema, and moderate lympholeucocyte infiltration. Well-formed promastigotes without flagella and also leishmanial forms with a typical inner structure were seen among the cell elements of the infiltration. In animals killed after 24–27 hours, the infiltrations had typical leishmanial forms and many dying parasites without a distinct outline and with pycnotic nuclei. After 2–4 days, leishmanial forms were not found but chromatin granules and clusters which seemed to be disintegrated leishmanias were seen. From the 5th or 7th day the inflammation gradually disappeared. Experiments with white mice showed similar histological changes in the skin.

The transformation of gecko promastigotes into the leishmanial form in the skin of warm-blooded animals in the course of the first days of infection is proof of a certain affinity between reptilian promastigotes and true leishmanias. It is partially confirmed by comparative studies of a number of other properties of reptilian leishmanias and promastigotes (the reaction of cultures grown on N.N.N. medium to different temperatures, the mode of growth on the medium supplemented with homologous and heterologous sera, behaviour in chicken embryo and tissue cultures). However, after the results of all major studies have been reviewed, promastigote strains from reptiles must be considered as non-pathogenic for warm-blooded organisms. It can be assumed that reptilian promastigotes were of importance in the formation of natural foci of leishmaniasis in the past and that modern species of pathogenic leishmanias originated from reptilian promastigotes and gradually became adapted to warm-blooded hosts.

RÉSUMÉ

LES REPTILES ET LEUR IMPORTANCE DANS L'ÉPIDÉMIOLOGIE DE LA LEISHMANIOSE

L'étude de la leishmaniose chez les reptiles présente un grand intérêt du fait que l'on a isolé, à de nombreuses reprises, des promastigotes d'une variété de lézards et que les phlébotomes se nourrissent avec facilité sur les lézards.

L'auteur a recueilli des *Leishmania* de lézards au cours de l'hiver, ce qui démontre que les lézards peuvent demeurer infectés dans la nature pendant les saisons où les phlébotomes sont inactifs. On peut donc conclure que l'infection se maintient longtemps, peut-être durant la vie entière du lézard hôte. Il est intéressant aussi de signaler le très petit nombre de parasites présents dans les étalements sanguins ou les empreintes de tissus. L'auteur a observé des promastigotes dans les étalements sanguins ou les empreintes tissulaires de quatre échantillons seulement; deux de *Phrynocephalus interscapularis* et deux d'*Agama sanguinolenta*. Cependant, des 3818 lézards (6 familles, 21 espèces) et des 9 serpents examinés pendant la période 1963-1966, de nombreux isolements ont été faits en milieux de culture. On a recueilli des flagellés de 11 des 21 espèces de lézards examinés: 6 d'entre eux *(Gymnodactylus caspius, A. sanguinolenta, P. interscapularis, P. mystaceus, Eremias intermedia*, et *E. grammica)* étaient déjà reconnus comme hôtes; 5 l'ont été pour la première fois en URSS *(Tetrascincus scincus, P. r. raddei, E. velox, E. g. guttulata, E. lineolata)*. Tous, sauf *E. lineolata*, avaient déjà été reconnus comme hôtes hors de l'URSS. De nombreux isolements ont été faits sur plusieurs de ces espèces. On a enregistré des taux d'infection de 20-30% pour *Gymnodactylus caspius* et de 14,5% pour *Agama sanguinolenta*.

L'absence d'une forme amastigote intracellulaire est aussi intéressante. Cela suggérerait que le parasitisme intracellulaire a commencé assez tardivement au stade du lézard dans l'évolution parasitaire et qu'il s'est agi d'une forme établie seulement lorsque le parasite s'est adapté à ses hôtes, mammifères à sang chaud.

L'auteur a pu démontrer qu'il n'existait pas de transmission transovarienne chez le phlébotome.

La survie de souches *Leishmania* du lézard dans la peau de l'homme et des rongeurs hôtes est passagère et localisée. Même si des formes amastigotes apparaissent brièvement, leur noyau devient pycnotique et elles commencent à mourir environ 27 heures après, pour disparaître totalement au bout de 2-4 jours. Des résidus granuleux peuvent être observés après 5 jours dans certaines parties de la peau des rongeurs.

Des cultures de souches humaines et de souches de gerbille pathogènes ont été inoculées à 14 espèces de lézards. On a aussi soumis à des tests des souches humaines isolées de phlébotomes et maintenues en culture, ainsi que des souches provenant de lézards. On a constaté chez les lézards une très faible réceptivité à l'égard de toutes les souches sauf une; il s'agissait d'une souche morphologiquement distincte provenant de *Phrynocephalus interscapularis*. On a retrouvé chez des lézards de 5 espèces (*A. sanguinolenta, G. caspius, E. lineolata, E. intermedia, E. velox*) des souches de promastigotes qui leur avaient été inoculées. On a obtenu des résultats positifs chez quatre espèces de lézards (*A. sanguinolenta, G. caspius, E. intermedia, P. interscapularis*) auxquels on avait inoculé des cultures de leishmaniose viscérale humaine. Il en était de même chez un lézard (*G. caspius*) auquel on avait inoculé des promastigotes de phlébotomes.

La capacité des *Leishmania* de lézard à devenir des amastigotes chez les mammifères, formes qu'elles ne prennent pas chez leurs hôtes lézards habituels, présente un intérêt considérable du point de vue théorique. En effet, on pourrait en déduire qu'il existe un rapport entre les parasites de la leishmaniose de différents mammifères hôtes et une aptitude des promastigotes de lézard à prendre la forme intracellulaire typique des hôtes à sang chaud.

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