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Wellcome Laboratories of Tropical Medicine, London.

Vampire Bats as Vectors and Hosts of Equine and Bovine Trypanosomes.*

By CECIL A. HOARE, F.R.S.

“But first, on earth as vampire sent,
Thy corse shall from its tomb be rent:
Then ghastly haunt thy native place,
And suck the blood of all thy race.”

BYRON. *Giaur*. 1813.

I. Introduction.

In Central and South America there are two related forms of trypanosomiasis, Murrina and Mal de Caderas, affecting domestic equines and bovines. They are normally transmitted by Tabanid flies which act as mechanical inoculators but, in addition to these insect-vectors, the causative organisms of these diseases, *Trypanosoma hippicum* and *T. equinum*, respectively, are also transmitted by Vampire bats (*Desmodus rotundus*). The transmission of blood parasites to a mammal of one order (Ungulata) by a mammal of another order (Chiroptera) represents an exceptional and paradoxical phenomenon in parasitology, that does not fit into the conventional parasite-vector-vertebrate pattern characteristic of transmissible infections, such as trypanosomiasis. From this category we can exclude Dourine, which is thought to have lost its vector in the course of evolution, with the result that the parasite, *T. equiperdum*, is now transmitted by direct contact between vertebrate hosts of the same species, viz. horses (HOARE, 1948).

Since Vampire bats play an important role in the spread of at least two types of trypanosomiasis among domestic ungulates of Latin America, I propose to consider the epizootology of these diseases and the part played by the bats in their transmission.

II. Trypanosomiasis of Ungulates in Latin America.

In the tropical and subtropical zones of America there occur four types of trypanosomiasis affecting domestic ungulates: (a) Secadera, caused by *T. vivax*, (b) Murrina, caused by *T. hippicum*, (c) Mal de Caderas, caused by *T. equinum*, and (d) Desrengadera or Peste Boba, due to *T. venezuelense*. Since Vampire bats are not involved in the transmission of Secadera, and the independence of Desrengadera is doubtful, they need not be dealt with here. Both Murrina and Mal de Caderas are diseases mainly of equines, whereas bovines are symptomless carriers of the in-

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fections. These two diseases have similar clinical symptoms, comparable to those of Surra (*T. evansi*) in the Old World. In horses the disease runs an acute or chronic course, and may acquire an epizootic character with high mortality.

The trypanosomes causing these diseases (Fig. 1) belong to the *brucei*-group or subgenus *Trypanozoon* (HOARE, 1964, 1965). One of them, *T. hippicum*, is indistinguishable from *T. evansi* and should therefore be placed in the latter species as a synonym (HOARE, 1949), while *T. equinum*, which is probably an "akinetoplasmic" mutant race of *T. evansi* (HOARE, 1954, 1960), can be regarded as an independent species. In addition to these species, some authors recognize *T. venezuelense* as the causative agent of Desrengadera but, since both morphologically and geographically this parasite occupies an intermediate position between *T. evansi* (= *T. hippicum*) and *T. equinum*, it is conceivable that infections with *T. venezuelense* might be due to a mixture of the two last-named species (HOARE, 1949).

These trypanosomiasis provide an example of transmissible diseases that had been introduced into a new country with their vertebrate hosts through human agency (HOARE, l.c.). As

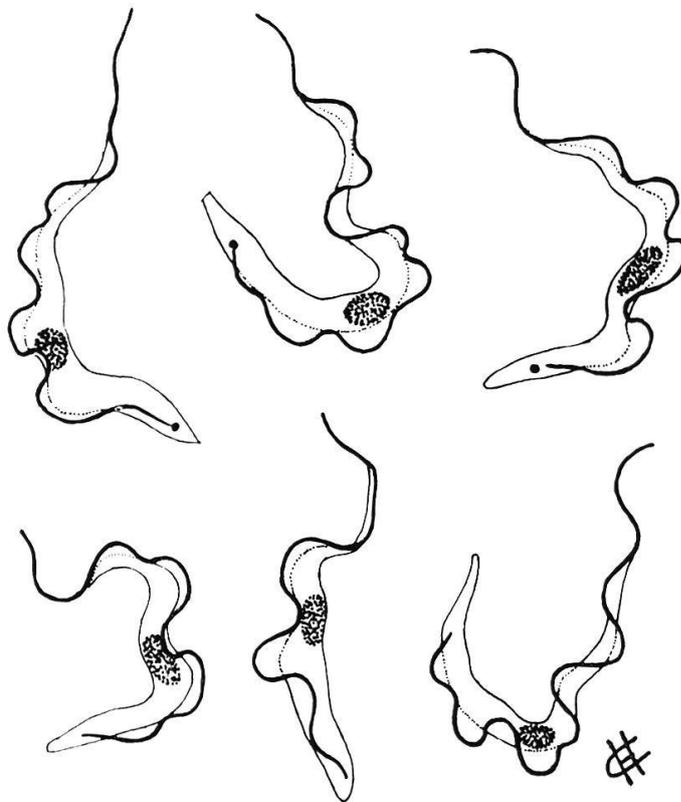


Fig. 1. Equine trypanosomes transmitted by Vampire bats ($\times 2,000$). Upper row: *Trypanosoma hippicum* (= *T. evansi*); lower row: *T. equinum*. (Original.)

is known, horses were absent in the New World before the XVI century, when they were brought to Latin America by the Spanish conquistadores with their cavalry. In the course of time some of the imported animals must have escaped and gone wild, eventually giving rise to the herds of mustangs and baguales which roamed widely over the pampas. It can be assumed that among the imported animals there were occasionally carriers of *T. evansi* (= *T. hippicum*), from which the infection spread among the domestic and feral horses, producing outbreaks of Surra, which later became known as Murrina. In this connexion it is significant that the mounts of the conquistadores were descended from horses which had been regularly introduced to Spain from the Barbary Coast of Africa, where equine Surra ("Debab") has always been enzootic. As regards Mal de Caderas, there is evidence that the infection was first observed between 1827 and 1830 on the island of Marajo, near the estuary of the Amazons (JANSEN, 1941), whence *T. equinum* spread over Brazil, giving rise to severe epizootics among horses. Like the equines, bovines also were not indigenous to the New World. According to BREHM (1916), they were first introduced by Columbus, during his second expedition (1493) to Santo Domingo, where they multiplied rapidly. Regarding the introduction of cattle to South America there are two versions: according to one, they were imported from Santo Domingo in 1540; according to the other, in 1546 Captain Juan de Salasa brought over from Andalusia to Brazil only seven cows and one bull. Whichever the case may be, it would seem that the herds which subsequently spread all over South America were the descendants of imported Spanish cattle.

The diseases in question have a wide geographical distribution in Latin America. Thus, the area of Murrina (*T. hippicum* = *T. evansi*) comprises Mexico, all Central America, Venezuela and Colombia, while the area of Mal de Caderas (*T. equinum*) occupies the greater part of South America, especially Brazil. As in the case of *T. evansi* in the Old World, the usual vectors of *T. hippicum* and *T. equinum* are horse-flies (KELSER, 1939; JANSEN, 1941; BOEHRINGER & PROSEN, 1961). These insects are typical mechanical inoculators (BEKLEMISHEV, 1955) whose ability to transmit the infection to new vertebrate hosts depends on interrupted feeding. However, as shown in a previous paper (HOARE, 1957), mechanical transmission of *T. evansi*—as well as of its descendents, *T. hippicum* and *T. equinum*—has probably evolved as a secondary adaptation when this species had separated from its African ancestor, *T. brucei*, and lost its original intermediate host, the tsetse-fly (*Glossina*).

After *T. evansi* (= *T. hippicum*) and *T. equinum* established themselves in the New World, they acquired—in addition to blood-sucking flies—a new type of vector, viz. Vampire bats, the role of which in the transmission of the trypanosomiasis is considered below.

III. Role of Vampires in the Epizootology of Trypanosomiasis.

(a) Description of Vampire Bats.

The true Vampires are represented by sanguivorous bats of the family Desmodontidae, comprising three genera and species, *Desmodus rotundus*, *Diphylla centralis* and *Diaemis youngi*. Since the last two species are not concerned with the transmission of trypanosomiasis, we shall restrict ourselves to *Desmodus*.

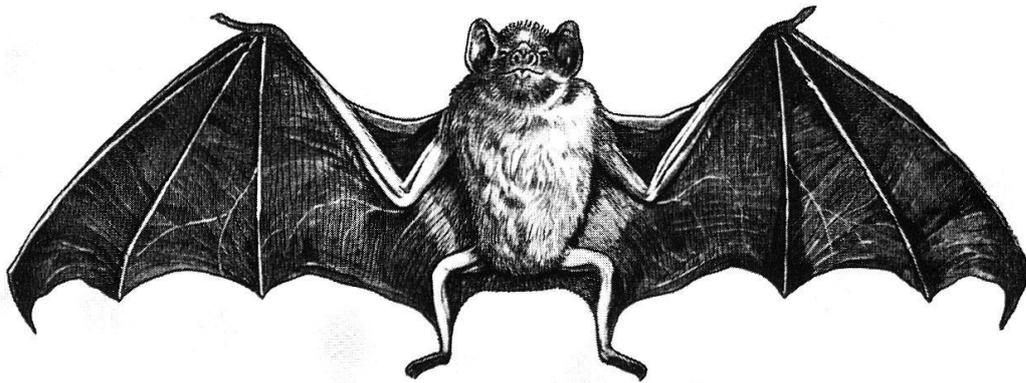


Fig. 2. Vampire bat, *Desmodus rotundus*. (From CABRERA & YEPES, 1940.)

The word *vampire* is of southern Slavonic origin, and has been used in this and other forms (e.g. Russian *upyr*, Greek *vrykolakas*: hence Turkish *vrkolak* and Russian *vurdalak*) in different countries from times immemorial to denote the superstitious belief in the existence of deceased persons of a malignant nature, whose animated corpses continue to live in the grave. They are supposed to issue forth nightly in order to attack sleeping human beings and suck their blood, whereby the vampires are nourished and revitalized, while their victims are destroyed and eventually also transformed into vampires. The vampire legend has inspired numerous poems, plays and novels in different languages, and the belief and interest in vampirism still lingers in superstitious minds (an exhaustive account of this phenomenon will be found in a book by

SUMMERS, 1928). In medico-legal practice the term vampirism has been extended to those blood-thirsty criminals, who—in order to satisfy their unnatural craving—murder their victims by biting them in the throat and then suck their blood (cf. SUMMERS, 1928, and VILLENEUVE, 1956).

The existence of sanguivorous bats in the Western Hemisphere became known to Europeans only since the discovery of the island of Trinidad by COLUMBUS at the end of the XV century, but the

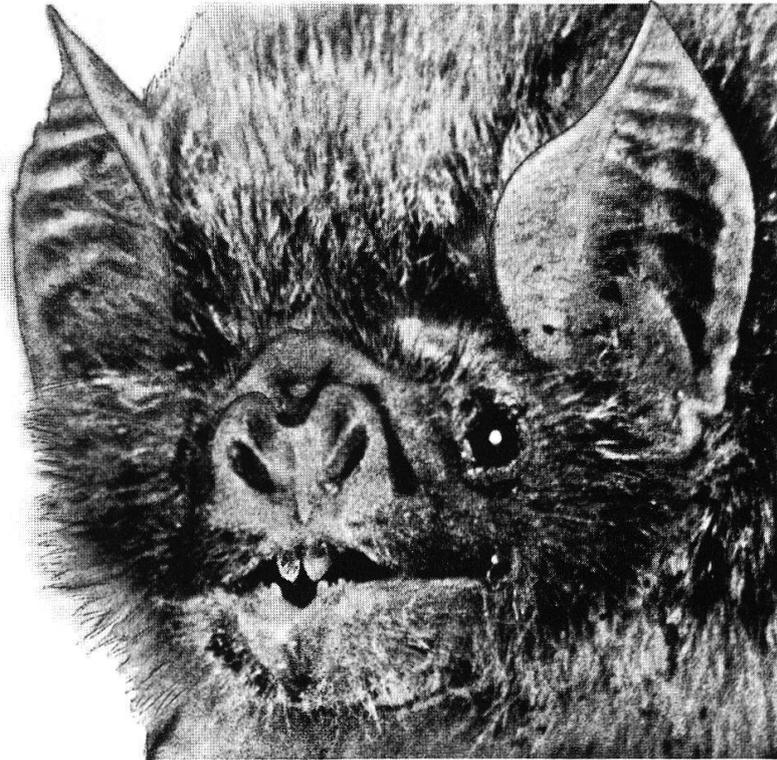


Fig. 3. Head of Vampire bat. (From WALKER, 1964.)

tales about these bats apparently first reached Europe in the XVI century, when followers of the Spanish conquistadores began to return from Central and South America. Subsequently the stories about blood-sucking bats combined with the local superstitions, with the result that the legendary Vampires were endowed with bat's features, while their name was transferred to the American bats. The early naturalists (including HUMBOLDT), who visited Latin America and heard about haematophagous bats, erroneously attributed this habit to the largest and ugliest of them. The first exact observation of the feeding habits of these bats was made by CHARLES DARWIN (1839) during his voyage on *H.M.S. Beagle*. In 1832, when visiting Chile, he not only succeeded in catching a bat in the act of gorging itself with blood on the withers

of a horse, but also identified it correctly as belonging to the genus *Desmodus* (DARWIN, 1845). Later, a study of the dentition and of the intestinal contents of *Desmodus* convinced HENSEL (1869) that these were the only sanguivorous bats. In spite of the conclusive observations by DARWIN and HENSEL, many naturalists continued to attribute blood-sucking habits to innocent bats, among which may be mentioned the misnamed *Vampyrum*, while popular imagination invested them with demoniac characters.

We now have exact data regarding *Desmodus rotundus* (Figs. 2, 3) whose area of distribution comprises the greater part of the Neotropical and the southern part of the Nearctic regions, where these bats are widespread from northern Mexico to southern Argentina, as well as in the West Indies. The territory occupied by Vampire bats thus coincides with the geographical distribution of Murrina and Mal de Caderas.

The Vampires are small animals, measuring about 7.5-9 cm. in length, while their wing-spread is about 33 cm. They have a very characteristic dentition (DITMARS & GREENHALL, 1935; DE VERTEUIL & URICH, 1936; WALKER, 1964), which is specially adapted for cutting (Fig. 4): the pair of upper chisel-like incisors are extremely sharp and curved to form a scoop-like mechanism, while the lower incisors are widely separated to form a groove along which the tongue moves during the act of feeding. The upper canines play no part in inflicting the wound but serve as supports to keep the head in position. The alimentary tract (including stomach) is represented by a narrow convoluted tube adapted to rapid digestion of the blood, which is the only food of these animals. In contrast to other bats, which can only crawl helplessly on their belly with outstretched wings, the Vampires are as agile as any other quadruped. When walking, their wings are folded tightly in fan-like fashion and serve as forelimbs, while the hindlimbs are directed backwards, and the whole body is raised about 2 inches above the ground.

The Vampire bat attacks its victim during the night, when it alights on the sleeping animal and walks leisurely to the site of choice, usually the shoulder or withers. There it might first clip off some of the hair to clear a small space and then it makes a quick cut in the skin with the razor-edged upper incisors, producing a shallow wound covering an area of about 7×4 mm and 1-5 mm deep. As the blood oozes out of the wound, the bat laps it up with its tongue which darts in and out of the mouth like a piston; but if the blood does not flow freely, the tongue is sometimes applied to the wound itself or a new incision is made. Thus the Vampire does not suck the blood with its mouth, as was popularly be-

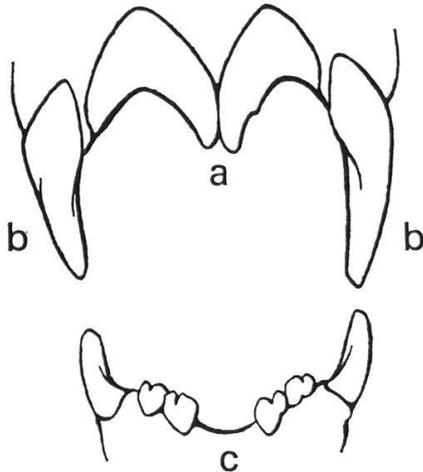


Fig. 4. Dentition of Vampire bat. a) Upper incisors, which inflict wound; b) Upper canines, which support head when feeding; c) Groove between lower incisors, through which tongue moves when lapping blood. (From DE VERTEUIL & URICH, 1936.)

lieved, but licks it up with its tongue (DUNN, 1932). The bat may take up from 16 to 50 ml of blood during its meal (CLARK & BENAVIDES, 1935; ENRIGHT, 1956; CLARK, 1948). Moreover, the presence in its saliva of an anticoagulant prevents the blood from clotting, thereby prolonging the bleeding and enabling the bat to feed for about 30 minutes without interruption. The bite of the Vampire is so painless that the victim is not disturbed during the repast, the only evidence of which may be provided by blood stains. Having gorged itself, the Vampire flies away to a sheltered place, such as a cave or hollow tree, where it spends the day hanging head downwards and digesting its food.

(b) Relation of Vampires to Trypanosomiases

The susceptibility of Vampire bats to infection with the trypanosomes of Ungulates has been studied chiefly in the case of *T. hippicum* (= *T. evansi*). Working in Panama, DUNN (1932) and JOHNSON (1936 a, b) provided experimental proof that the bats which had fed on the blood of horses suffering from Murrina become infected with this parasite. They also demonstrated that, in order to gain access to the recipient's blood, the trypanosomes which had been ingested with the donor's blood must first penetrate into the oral mucous membrane of the bat. Moreover, in a number of cases Vampires have been found naturally infected with *T. hippicum*. The infection in the bats usually lasts about one month and may terminate fatally, but in some cases the animals survive and recover spontaneously (CLARK, 1948).

In a series of experiments by the American workers, Murrina was successfully transmitted to horses and mules by allowing in-

fecting bats to bite them. The mechanism of the transmission of *T. hippicum* to equines is determined by the following factors: (a) by the ability of the trypanosomes present in the blood of infected bats to pass through the oral mucous membrane and thence into the mouth, where the parasites have actually been detected in the saliva; and (b) by the vulnerability of the buccal mucosa, the slightest injury to which likewise gives the trypanosomes access to the oral cavity (JOHNSON, 1936b). It is thus seen that the reciprocal transfer of the infection between equines and Vampires is facilitated by the fact that the oral mucous membranes of the bats presents no barrier to the parasites, enabling them to pass through it in both directions. The chances of successful transmission of the parasite by the Vampires also depend upon their method of feeding on the horse. Thus, if blood from the wound flows freely and the bat has only to lap it up, the conditions for transmission are not particularly favourable; but if bleeding is arrested and the bat is forced to lick the wound itself, the chances of transmission are considerably increased (ALLEN, 1939). Moreover, the bat can probably transmit the infection also during the act of biting.

Since the natural vectors of *T. hippicum*—like those of the Old World *T. evansi*—are typically horse-flies (Tabanidae), Murrina can be transmitted quite independently of Vampires, which do not therefore play any biological role in the life cycle of the parasite. In fact, Vampire bats are relatively recent hosts of the equine trypanosomes, having become involved only since Surra (now Murrina) was introduced to America with horses. After the horses spread to territories occupied by these bats, the latter began to feed on the blood of the new hosts and became infected with their trypanosomes. Subsequently, when infected Vampires attacked other horses, they transmitted Murrina to them. Thus, the Vampire was not included in the life cycle of *T. hippicum* as a necessary component but became associated with this parasite as a parallel and independent host (cf. BEKLEMISHEV, 1956), while serving at the same time as its vector (Fig. 5). However, the part played by Vampire bats as vectors is of considerable epizootological importance, especially during interepizootic periods, when the infection among equines dies out but is retained in cattle, which represent reservoir hosts of Murrina (CLARK et al., 1933; CLARK & BENAVIDES, 1935; JOHNSON, 1936b; CLARK, 1948). Thus, it was shown that in Panama up to 6% of the local cattle are symptomless carriers of *T. hippicum*; moreover the infection is typically so scanty that the presence of trypanosomes in the bovines can be detected only indirectly, by inoculation of susceptible laboratory

animals. Under these conditions, the Vampires represent ideal vectors, for their infection from cattle harbouring insignificant numbers of parasites is ensured by the large amount of blood consumed during a meal, while the intense proliferation of the trypanosomes in their own body increases the chances of successful transmission to new hosts. Owing to these peculiarities, Vampires play an important part in the spread of bovine Murrina among herds of horses. It is interesting that the difference in susceptibility to Murrina between American cattle and horses is similar to that observed in these hosts in the case of Surra in the Old World (HOARE, 1956).

Although fewer observations have been carried out on Mal de Caderas, it has been established that—as in the case of Murrina—Vampires serve as parallel hosts and vectors of this disease as well. Thus, it was demonstrated experimentally that in Argentina the sanguivorous bats become infected with *T. equinum* from horses and can transmit this parasite when feeding on healthy equines (ACOSTA & ROMAÑA, 1938; ROMAÑA, 1948). In Brazil Vampires were incriminated in causing an outbreak of Mal de Caderas (KUBIAK & MOLFI, 1953), and it has been shown, under experimental conditions, that these bats are susceptible to infection with *T. equinum* and are capable of transmitting the parasites by biting laboratory animals (JANSEN, 1941; OLIVEIRA, 1943).

IV. Discussion.

We can now consider the nature of the unusual host-parasite relations between the Vampire bats and the equine trypanosomes. As there is no recognized term to denote the unique combination of host and vector in the same animal, an appropriate name for Vampires acting in both these capacities might be “hospitovectors” (from *hospes* + *vector*). As regards the life cycle of *T. hippicum* and *T. equinum*, it is represented by two types (Fig. 5): (a) metaxeny (ROSS, 1911), characterized by a regular alternation of vertebrate and invertebrate hosts (in this case: ungulates and blood-sucking flies), and (b) paraxeny (from “paraxenosis”: MOSHKOVSKY 1943), characterized by the inclusion of a parallel host (in this case: vampire acting also as vector).

The dual role of Vampires as vectors and hosts has the following implications. Although they transmit the trypanosomes mechanically, they differ from typical mechanical inoculators in that the success of transmission does not depend upon the temporary survival of the parasites during the intervals between interrupted

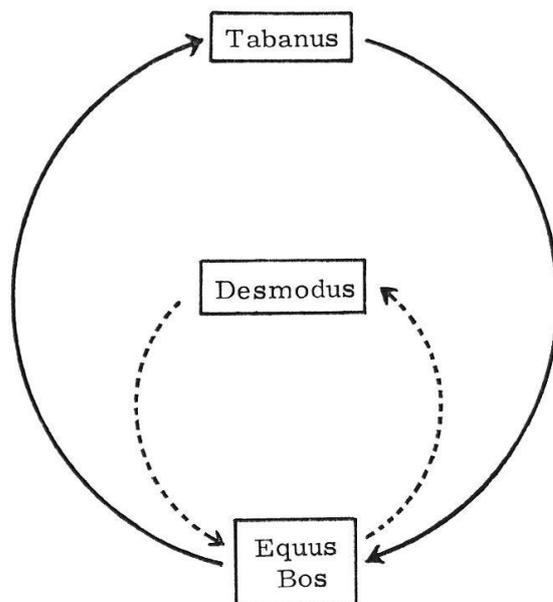


Fig. 5. Diagram showing life cycle of *Trypanosoma hippicum* and *T. equinum*. Circulation of the parasite is indicated by arrows; continuous lines indicate main cycle (metaxeny), involving insect-vector; interrupted lines indicate parallel cycle (paraxeny), involving Vampire bat. (Original.)

meals (as in the case of their insect-vectors). And indeed, owing to the persistence of the infection in the bats, they are capable of transmitting the parasites for relatively long periods of time. From the ecological point of view, Vampires belong to the category of vectors which transmit the infection by active contamination of wounds (BEKLEMISHEV, 1955). They differ from specific cyclical vectors in the fact that the parasites do not undergo in them a cycle of development characteristic of a true intermediate host, but multiply in their blood in the same way as they do in the natural vertebrate host. Lastly, in addition to being parallel or incidental hosts of the equine trypanosomes, Vampires also serve as reservoirs of these parasites, but again—unlike typical reservoir hosts—they also act as vectors of the infection.

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Zusammenfassung.

In Zentral- und Südamerika werden zwei verwandte Formen von Trypanosomiasen, Murrina und Mal de Caderas, welche Hauspferde und -rinder befallen, normalerweise von Tabaniden übertragen. Sie wirken als mechanische Überträger. Außer diesen Insekten-Überträgern können aber auch Vampir-Fledermäuse (*Desmodus rotundus*) die Krankheitserreger *Trypanosoma hippicum* (= *T. evansi*) und *T. equinum* übertragen. Diese Fledermäuse ernähren sich ausschließlich vom Blut von Säugetieren. Sie greifen sie nachts an, bringen ihnen eine kleine Wunde bei und lecken das herausfließende Blut mit der Zunge auf. Sie können bis zu 50 ml Blut während einer ungefähr 30 Minuten dauernden Blutmahlzeit aufnehmen. Es konnte nachgewiesen werden, daß Vampir-Fledermäuse, die sich mit Blut von an Trypanosomiasen erkrankten Pferden ernähren, infiziert werden. In den Fledermäusen kann die Krankheit einen akuten oder chronischen Verlauf nehmen, und sie wird durch nachfolgende Blutmahlzeiten auf gesunde Pferde übertragen. Die Infektion der Fledermäuse und die Übertragung der Trypanosomen durch diesen Wirt auf neue Opfer wird dadurch erleichtert, daß die Trypanosomen die Mundschleimhäute zu durchdringen vermögen: wird infiziertes Blut aufgenommen, so dringen sie nach innen, nähren sich die Fledermäuse aber auf neuen Wirten, so dringen sie nach außen in die Mundhöhle, wo sie im Speichel gefunden werden können. Vampire sind wichtige Überträger während interepizootischen Perioden, wenn die Krankheit hauptsächlich im Vieh latent gegenwärtig ist. In Viehherden können sich bis zu 6% symptomlose Träger befinden und so als Reservoir für die Infektion dienen. Die Krankheit wird dann durch die Fledermäuse vom Vieh auf neue Pferdeherden ausgestreut.

Die Übertragung von Blutparasiten auf Säugetiere einer Ordnung (Ungulata) durch Säugetiere einer andern Ordnung (Chiroptera) ist in der Parasitologie ein ungewöhnliches Phänomen, das nicht in das konventionelle Schema Parasit-Überträger-Wirbeltier (charakteristisch für die übertragbaren Infektionen wie Trypanosomiasen) hineinpaßt. Da die Vampir-Fledermaus nicht ein notwendiges Glied im Lebenszyklus von *T. hippicum* und *T. equinum* darstellt, wirkt sie als zufälliger oder paralleler Wirt für diese Trypanosomen, dient aber gleichzeitig auch als deren Überträger. Demnach haben die Trypanosomen, die Murrina und Mal de Caderas verursachen, einen zweifachen Lebenszyklus (der eine ist metaxenisch, der andere paraxenisch [Abb. 5]). Einerseits

entspricht die Rolle der Fledermäuse mechanischen Überträgern, doch sie unterscheiden sich von diesen dadurch, daß der Erfolg der Übertragung nicht vom zeitlichen Überleben der Parasiten zwischen mehreren Blutmahlzeiten abhängt. Andererseits unterscheiden sie sich aber auch von spezifischen Überträgern, indem die Parasiten in den Fledermäusen keine zyklische Entwicklung durchmachen müssen, sondern sich dort nur im Blut vermehren. Endlich, abgesehen von ihrer Rolle als parallele Wirbeltier-Wirte, können die Fledermäuse auch zugleich als Reservoir für die betreffenden Trypanosomen dienen, und, anders als Reservoir-Wirte, sind sie zudem auch noch Überträger der Infektion.

Résumé.

En Amérique Centrale et en Amérique du Sud, deux formes parentes de trypanosomiasés, Murrina et Mal de Caderas, affectant les cheptels bovins et équins, sont normalement inoculées mécaniquement par des Tabanides. A côté de cet insecte-vecteur, *Trypanosoma hippicum* (= *T. evansi*) et *T. equinum* sont également transmis par des vampires (*Desmodus rotundus*). Ces chauves-souris se nourrissent exclusivement du sang des mammifères auxquels elles s'attaquent nuitamment. L'animal lèche le sang coulant de la blessure qu'il a provoquée. Un repas sanguin d'environ 30 minutes lui permet de consommer jusqu'à 50 ml de sang. Il a été démontré que les vampires se nourrissant sur des chevaux atteints de trypanosomiase pouvaient s'infecter (l'infection se développant chez eux soit de manière aiguë, soit de manière chronique) et transmettre la maladie à des chevaux sains au cours d'un prochain repas. L'infection de la chauve-souris et la transmission du trypanosome par cet hôte sont facilitées par le fait que les parasites sont capables de traverser les muqueuses orales : une première fois lorsqu'ils infectent l'hôte lors de l'ingestion du sang parasité, une seconde fois lors de la transmission traversant les muqueuses en sens contraire, les parasites retournent dans la cavité buccale où on les trouve dans la salive.

Les vampires sont d'importants vecteurs de la trypanosomiase durant les périodes interépizootiques, alors que la maladie affecte principalement le bétail, dont 6% des têtes peuvent être des porteurs sans symptômes apparents, c'est-à-dire des réservoirs. La maladie est transmise par les vampires du bétail à de nouveaux troupeaux de chevaux.

La transmission d'un parasite sanguicole à un mammifère d'un certain ordre (Ungulata) par un mammifère d'un autre ordre (Chiroptera) est un phénomène inhabituel en parasitologie. Celui-ci n'entre pas dans le schéma conventionnel caractéristique de la transmission d'infections telle que la trypanosomiase, obéissant au jeu parasite-vecteur-vertébré. Comme le passage par le vampire n'est pas obligatoire dans le cycle de *T. hippicum* et de *T. equinum*, ce mammifère joue pour ces parasites le rôle d'hôte fortuit ou parallèle, un hôte qui sert en même temps de vecteur. Ainsi les trypanosomes causant la Murrina et le Mal de Caderas ont un double cycle : l'un métaxénique, l'autre paraxénique (Fig. 5). Comme vecteur, les vampires sont des inoculateurs mécaniques, mais différent de ceux-ci en ce sens que le succès de la transmission ne dépend pas de la survivance temporaire du parasite entre deux repas. Ils ne sont pas non plus vecteurs spécifiques puisque le parasite n'accouplit pas chez eux l'évolution cyclique caractéristique des hôtes intermédiaires, se contentant de se multiplier dans leur sang. Enfin, tout en étant un hôte parallèle, les vampires peuvent être des réservoirs dans des trypanosomes en question, mais — au contraire des autres réservoirs — ils sont aussi des vecteurs de l'infection.