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Parasitic Protozoa of the Blood of Rodents.
II. Haemogregarines, Malaria Parasites and Piroplasms
of Rodents: an Annotated Checklist and Host Index¹

ROBERT KILICK-KENDRICK

Abstract

The protozoa parasitic in the blood cells of rodents are listed with their known hosts and the countries in which they have been found. Haemogregarines of the genus *Hepatozoon* have been seen in 67 species of rodents; they are the commonest and most widespread blood sporozoa of sciuriforms and myomorphs. Most reports are from the Palaearctic, Ethiopian and Oriental regions. Gametocytes of the parasites inhabit leucocytes except the species parasitizing jerboas, gerbils, *Cricetomys*, *Dendromus* and *Otomys* which are in erythrocytes. Since the gametocytes are, with few exceptions, indistinguishable morphologically, and only few life-cycles have been seen, the true number of species parasitic in rodents is unknown.

Piroplasms of the genus *Babesia* are the next most common blood sporozoa of rodents, with records from 57 species. This parasite is especially prevalent in rodents of the Nearctic, Palaearctic and Ethiopian regions, but is not common in rodents of the Neotropical, Oriental and Australasian regions. Sciuriforms other than marmots are rare hosts, and most reports are from myomorphs, especially gerbils. The specific identity of many of the piroplasms is in doubt.

Among rodents, *Hepaticystis* has been found only in squirrels of the Oriental region, 16 species of which are known hosts. The related haemoproteid, *Rayella*, has been reported in 4 flying squirrels of India.

True malaria parasites (*Plasmodium*) are known from 5 African murines, 2 African anomalurines, the African brush-tailed porcupine and 5 species of Asian flying squirrels; they have not been found in rodents of the Neotropical region.

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¹ This work was presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy, University of London.

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Introduction

The protozoa of the erythrocytes or leucocytes of rodents lie in five of the families in the subphylum Sporozoa, namely Hepatozoidae, Plasmodiidae and Haemoproteidae (Telosporea; Eucoccida), and Babesiidae and Dactylosomidae (Piroplasmae; Piroplasmida). Trypanosomes, which are not dealt with in the present work, are common extracellular parasites of the blood of rodents. A checklist which includes the species infecting rodents is given by HOARE (1972).

In addition to the true protozoa parasitizing the blood-cells of rodents, there are a number of other organisms which share the same habitat. *Bartonella* STRONG et al., 1915, *Anaplasma* THEILER, 1910, *Grahamella* BRUMPT, 1911, *Haemobartonella* TYZZER & WEINMAN, 1939, and *Eperythrozoon* SCHILLING, 1925, are parasites of the erythrocytes of a great number of different mammals including many rodents. Their true affinities long remained in doubt, but *Bartonella* is now regarded as a bacterium (PETERS & WIGAND, 1955; PEREZ-ALVA & GUIN-TINI, 1957), and the others as rickettsiae (PHILIP, 1957; WEINMAN, 1957). Records of these organisms are not included in this checklist. They are common in rodents and are easily seen in blood films stained in Giemsa's stain, although less easily assigned to a genus (see TYZZER, 1942). They occur singly or in groups in or on erythrocytes and appear as small dots or rod-shaped bodies.

An apparently similar parasite of the leucocytes of voles was described by COLES (1914), who found it in an English *Microtus agrestis*. It was later seen in the neutrophils and eosinophils of *M. pennsylvanicus* in the U.S.A. and named *Cytoecetes microti* TYZZER, 1938. Possibly *Cytoecetes* should be grouped with *Ehrlichia*, a tick-borne virus of the lymphocytes of cattle (FOGGIE, 1962).

In the preparation of the checklist the exact identity of some of the rodents has given difficulty, but an attempt has been made to correct errors such as records from rodents totally unknown in the given locality. In a few reports, however, the name listed is little more than an informed guess. The names of some of the rodents have been changed over the period covered, and as far as possible generally accepted modern names have been substituted. Trinomials have been ignored in some groups when the authorities seem not to be in agreement.

To speculate on possible relationships between parasites, it is helpful if the relationships of the hosts are understood. The abundance and diversity of rodents makes this difficult, but WOOD's (1955) revision of the higher taxa (followed in the host-index) is valuable to workers interested in the hostal distribution of the parasites of rodents. He increased the number of suborders from the three pragmatic but non-phylogenetic suborders commonly recognised (Sciuromorpha, Myomorpha and Hystricomorpha) to seven less arbitrary groups. WOOD's revision met with strong support from SIMPSON (1959), who adopted the new classification and acknowledged that his earlier views on the suborders (SIMPSON, 1945) had become indefensible; they are, nevertheless, still accepted by some (e. g. ROSEVEAR, 1969).

Great significance cannot be placed on the geographical distribution suggested by some of the reports which in many instances simply reflect the distribution of protozoologists. The names of some countries are continually changing: I have used the ones I think will be most easily understood. In an attempt to present as complete a picture as possible I have included a number of unpublished records.

Checklist of the Protozoa in the Blood-Cells of Rodents

The numbers after the names of the hosts below refer to the rodents in the host-index in which common names are given, questions of the identity of some of the hosts are discussed, and records from each rodent are gathered together. The records for each genus of parasite are arranged in chronological order according to the date of naming, or, for unnamed species, the date of the first report.

Hepatozoidae

Hepatozoidae includes the genus *Hepatozoon* MILLER, 1908, a widespread parasite of the leucocytes, or in a few instances (indicated by an asterisk [*] before the name in the checklist) the erythrocytes, of rodents and many other vertebrates. The only stage in the blood is the characteristically banana-shaped gametocyte. The haemogregarines of rodents have been given several different generic names, but I have referred them all to the genus *Hepatozoon*. Except for differences in size and host-cell, almost all the gametocytes look very much alike, and the few life-cycles which have been studied (e.g. *H. muris*, *H. pitymysi*, *H. balfouri*, *H. griseisciuri*, *H. erhardovae*) are typical of the genus *Hepatozoon*. At the moment there is little reason to suppose that true haemogregarines of rodents are represented by more than this one genus, although one of the haemogregarines of the pygmy flying squirrel (*Idiurus macrotis*) of the Ivory Coast (KILLICK-KENDRICK & BELLIER, 1971) looks more like genus *Haemogregarina* than *Hepatozoon*.

Possibly some of the *Hepatozoon*-like parasites of rodents are not haemogregarines at all, but extra-intestinal forms of *Isospora* of cats or other carnivores. FRENKEL & DUBEY (1972) described haemogregarine-like stages of *I. felis* and *I. rivolta* in the lymph nodes of laboratory rats, mice and hamsters which had been fed oocysts. This led MARKUS (1973) to remark that records of haemogregarines should be re-examined. But the extra-intestinal forms of feline coccidia have yet to be described in the peripheral blood of experimentally infected rodents. Even if they are, a distinction should perhaps be made between haemogregarines of erythrocytes and those of leucocytes, since the former seem unlikely to be stages of intestinal coccidia of cats.

There is some confusion in the naming of the species of *Hepatozoon* of rodents, caused by the old practice of calling all haemogregarines of murids, *muris*. In the checklist I have used names given usually because of differences of host; this gives identities to haemogregarines which may later be shown not to deserve them.

1. **Hepatozoon balfouri* (LAVERAN, 1905); *Jaculus gordonii* (128) **Sudan** (BALFOUR, 1905, 1906); *J. orientalis* (129) **Tunisia** (LAVERAN, 1905a), **Egypt** (HOOGSTRAAL, 1961); *J. jaculus* (130) **Sudan** (BALFOUR, 1905, 1905), **Egypt** (HOOGSTRAAL, 1961; FURMAN, 1966)
2. *Hepatozoon muris* (BALFOUR, 1905); *R. norvegicus* (107) *R. rattus* (108) cosmopolitan; *Rattus assimilis* (105), *R. conatus* (106) **Queensland, Australia** (MACKERRAS, 1969).

As rats have moved around the world in the company of man, their haemogregarine has moved with them. Early records of *H. muris* were listed by KUSAMA et al. (1919), and more recently KRAMPITZ (1964) published a map showing 39 localities in **Europe, Asia, Australasia** and **N. and S. America** from which *H. muris* has been reported in *Rattus*. The common identity of the haemogregarines of species of *Rattus* has not been confirmed by transmission experiments in the laboratory.

H. perniciosum MILLER, 1908, a parasite of white laboratory rats (*R. norvegicus*) and the type species of *Hepatozoon* MILLER, 1908 is a synonym of *H. muris* (WENYON, 1926; BRUMPT, 1946).

3. **Hepatozoon gerbilli* (CHRISTOPHERS, 1905); *Tatera indica* (81) **Madras, India** (CHRISTOPHERS, 1905); *Rhombomys opimus* (89) **U.S.S.R.** (ZASUKHIN et al., 1935); *Tatera indica ceylonica* (82) **Ceylon** (MANAWADU, unpublished).
4. *Hepatozoon funambuli* (PATTON, 1906); *Funambulus pennanti* (4) **India**.
5. *Hepatozoon musculi* (PORTER, 1908); *Mus musculus* (119) **England** (PORTER, 1908), **Italy** (SANGIORGI, 1912), **U.S.S.R.** (YAKIMOFF & SCHOKHOR, 1917; ZASUKHIN, 1936), **Czechoslovakia** (ERHARDOVA, 1955).
WENYON (1926) believed that it was 'not improbable' that *H. musculi* was the same as *H. muris*.
6. *Hepatozoon citellicolum* (WELLMAN & WHERRY, 1910); *Citellus beecheyi* (33) **U.S.A.**
7. *Hepatozoon* sp. KLEINE, 1910; *Mylomys dybowski* (98) **Tanzania**.
8. *Hepatozoon criceti* (NÖLLER, 1912), *Cricetus cricetus* (65) **Austria**.
9. *Hepatozoon mereschkowskii* TARTAKOWSKY, 1913; *Citellus guttatus* (35) *C. musicus* (36) **U.S.S.R.**
10. *Hepatozoon arvalis* (MARTOGLIO, 1913); *Arvicanthis niloticus* (?) (99) **Ethiopia**.
MARTOGLIO identified the host as *Arvicola* (= *Microtus*) *arvalis* but, except for *M. guentheri* which is known from **Libya**, voles are absent from **Africa** (ELLERMAN & MORRISON-SCOTT 1966). BRUMPT (1946) suggested MARTOGLIO's rodent was perhaps *Arvicanthis abyssinicus* (= *A. niloticus*), and his parasite the same as *H. arvicanthis* SCHWETZ & COLLART, 1930.
LAVIER (1921) found a haemogregarine which he called *H. arvalis* in an undoubted *Microtus arvalis* collected in **France**. BRUMPT (1946) recognised LAVIER's parasite as new, and named it *H. lavieri*.
11. *Hepatozoon plicatum* (MARTOGLIO, 1913); *Pectinator spekei* (?) (51) **Somali Republic**.
12. *Hepatozoon* sp. RODHAIN, PONS, VANDENBRANDEN & BEQUAERT, 1913; rodent (see note in the host-index under Fam. Dipodidae), Sankisia, Congo-Kinshasa (**Zaire**).
13. *Hepatozoon microti* (COLES, 1914); *Microtus agrestis* (72) **England** (COLES, 1914; JACOBS, 1953), **Czechoslovakia** (ČERNA, 1957), **Germany** (KRAMPITZ, 1964), **Austria** (MAHNERT 1972); *Microtus* sp. (?) (79) **Volga Delta, U.S.S.R.** (DUBININ, 1953).
14. *Hepatozoon sciuri* (COLES, 1914); *Sciurus vulgaris* (2) **England** (COLES, 1914; VIZOSO, quoted by DASGUPTA & MEEDENIYA, 1958), **China** (NAUCK, 1927), **Italy** (FRANCINI, 1932), central and southern **Europe** (KRAMPITZ, 1964).
DASGUPTA & MEEDENIYA (1958) described sporocysts of an *Hepatozoon* in the flea *Orchopeas wickhami* from English squirrels. They examined fleas from both *S. carolinensis* and *S. vulgaris* but since the sporocysts contained twelve sporozoites, not four as in *H. griseisciuri* of *S. carolinensis*, their description is presumably of the sporogonic stages of *H. sciuri* of *S. vulgaris*.
15. *Hepatozoon sylvatici* (COLES, 1914); *Apodemus sylvaticus* (93) **England** (COLES, 1914), **W. Germany** (KRAMPITZ, 1964), **France** (RIOUX & GOLVAN, 1969); *Apodemus flavicollis* (92) **Czechoslovakia** (ERHARDOVA, 1955), central and southern **Europe** (KRAMPITZ, 1964); *Apodemus* spp. (94) **Austria** (MAHNERT, 1972).
16. *Hepatozoon akodoni* (CARINI & MACIEL, 1915); *Akodon fuliginosus* (60) São Paulo, **Brazil**.
17. *Hepatozoon pitymysi* Splendore, 1918; *Pitymys savii* (70) **Italy** (SPLENDORE, 1918; 1920) **Sicily** (KRAMPITZ, 1957).
LAVIER's (1921) suggestion that the haemogregarines of *M. arvalis* and *P. savii* were the same is not supported by the work of KRAMPITZ (1964), who demonstrated a marked host restriction of one of the haemogregarines of voles. Possibly these parasites are similar to the large group of *lewisi*-like trypanosomes of rodents which are morphologically indistinguishable but which exhibit strong host restrictions (e.g. MOLYNEUX, 1969).
18. *Hepatozoon getulum* SERGENT, 1921; *Atlantoxerus getulus* (27) **Tunisia**.
LANDAU (personal communication) found gametocytes of two unidentified haemogregarines, one large and one small, in the leucocytes of *A. getulus* from **Algeria**.

19. *Hepatozoon* sp. (LÉGER, 1922); *Euxerus erythropus* (30) **Senegal**.
20. *Hepatozoon* sp. DONOVAN (WENYON, 1926); *Petaurista petaurista* (44) **India**.
This record is in WENYON's checklist under the host's old name *Pteromys petaurista*: DONOVAN's report was apparently unpublished.
21. *Hepatozoon arvicanthis* SCHWETZ & COLLART, 1930; *Arvicanthis niloticus* (99) Congo-Kinshasa (**Zaire**).
22. *Hepatozoon lusitanicum* NAJERA ANGULO, 1937; *Eliomys quercinus* (136) **Spain**.
23. *Hepatozoon* sp. TYZZER, 1939; *Microtus pennsylvanicus* (78) Island of Martha's Vineyard, Mass., U.S.A.
24. **Hepatozoon alactagae* ZASUKHIN, 1936; *Alactagulus pumilio* (133) **Saratov Prov., U.S.S.R.** (ZASUKHIN, 1931, 1936); *Allactaga major* (131) **Saratov Prov., U.S.S.R.** (SHINGAREVA, 1910), **W. Kazakhstan, U.S.S.R.** (ZASUKHIN, 1936); *Styloidipus telum* (134) **Kalmyk Prov., U.S.S.R.** (ZASUKHIN, 1936); *Allactaga sibirica* (132), *Dipus sagitta* (127); **Mongolia and Manchuria** (JETTMAR, 1932).
BRUMPT (1946) gave the name *H. alactaguli* to the haemogregarine reported by ZASUKHIN (1931) in *Alactagulus acotion* (= *A. pumilio*), apparently unaware that ZASUKHIN (1936) had already named it *H. alactagae*. Complete life-cycles should be seen and cross infectivity tests performed to discover if more than one species of *Hepatozoon* is present in these jerboas.
25. *Hepatozoon arvicolae* BRUMPT, 1946; *Microtus montebelli* (?) (76) **Japan** (MIYAIRI, 1932).
26. **Hepatozoon cricetomysi* BRUMPT, 1946; *Cricetomys gambianus* (90) Congo-Kinshasa (**Zaire**) (RODHAIN, 1915), **Central African Republic** (LANDAU, unpublished).
27. **Hepatozoon dendromusi* BRUMPT, 1946; *Dendromus ?insignis* (125) **Tanzania** (KLEINE, 1910).
In spite of confusion, the correct spelling of the name of this rodent is apparently *Dendromus* not *Dendromys* (SIMPSON, 1945, ROSEVEAR, 1969). BRUMPT incorrectly called the host *Dendromys* (following KLEINE, 1910), and the parasite *H. dendromysi*. This error was caused by the current misspelling of the rodent's name, and the spelling of the name of the parasite is here corrected; an application is being made to the International Commission on Zoological Nomenclature.
28. *Hepatozoon graomysi* BRUMPT, 1946; *Graomys medius* (61) **Argentina** (ROMAÑA, 1945).
BRUMPT misspelt the name of the rodent and named the parasite *H. groamysi*. This was apparently an inadvertent error, and the spelling is here corrected; an application is being made to the International Commission on Zoological Nomenclature.
29. *Hepatozoon lavieri* BRUMPT, 1946; *Microtus arvalis* (74) **France** (LAVIER, 1921), **Czechoslovakia** (ERHARDOVA, 1955; ČERNA, 1957), **Austria** (KRAMPITZ, 1964).
30. *Hepatozoon* sp. LATYSHEV, 1949; *Meriones erythrourus* (85) **Turkmenia U.S.S.R.**
31. *Hepatozoon* sp. LATYSHEV, 1949; *Spermophilopsis leptodactylus* (32) **Turkmenia, U.S.S.R.**
32. *Hepatozoon* sp. (DUBININ, 1953); *Arvicola terrestris* (69) **Volga Delta, U.S.S.R.**
DUBININ (1953) thought this haemogregarine was perhaps *H. arvalis* (10), the parasite which MARTOGLIO (1913) recorded from a rodent misidentified as *Microtus arvalis*. KRAMPITZ's (1964) work suggests a host restriction of the haemogregarines of voles, and it is likely that DUBININ's parasite was new.
33. *Hepatozoon* sp. ERHARDOVA, 1955; *Microtus oeconomus* (77) **Czechoslovakia** (ERHARDOVA, 1955), central and southern **Europe** (KRAMPITZ, 1964), **Alaska, U.S.A.** (OHYASHI, 1971).
34. *Hepatozoon griseisciuri* CLARK, 1958; *Sciurus carolinensis* (1) **Maryland, U.S.A.** (HERMAN & PRICE, 1954, 1955; CLARK, 1958), **Rhode Island, U.S.A.** (WEIDANZ & HYLAND, 1958) **Wisconsin U.S.A.** (DORNEY & TODD, 1959), **Virginia U.S.A.** (PARKER, 1968), **England** (VIZOSO, quoted by DASGUPTA & MEEDENIYA, 1958).
CLARK (1958) and REDINGTON & JACHOWSKI (1971) found that the sporocysts of *H. griseisciuri* in the mites *Euhaemogamasus ambulans* and *Echinolaelaps echidninus* (= *Haemogamasus reidi*) contained only 4 large sporozoites and in this character the haemogregarine of the grey squirrel differs from other species.
35. *Hepatozoon* sp. RICHARDS, 1961; *Sciurus niger* (3) **Georgia, U.S.A.**

36. *Hepatozoon leptosoma* WOOD, 1962; *Peromyscus maniculatus* (58) **California, U.S.A.**

The gametocytes of this parasite differed from those of other Californian rodents by their larger size and more slender shape.

37. *Hepatozoon* sp. WOOD, 1962; *Microtus californicus* (75) **California U.S.A.**

WOOD (1962) tentatively identified this haemogregarine of a vole as *H. citellicolum* (6), a parasite of the gopher, *Citellus beecheyi*. These hosts are not closely related and until the life-cycles of the parasites are compared, WOOD's *Hepatozoon* of *M. californicus* is better left with a separate identity.

38. *Hepatozoon* sp. WOOD, 1962; *Peromyscus boylii* (56), *P. truei* (59) **California, U.S.A.**

WOOD (1962) thought this haemogregarine was probably *H. muris* (2), a parasite of *Rattus* spp. From the host restriction of the better studied haemogregarines of European rodents (KRAMPITZ, 1964), it seems probable that Wood's parasite was new. Morphologically its gametocytes differed from those of the haemogregarines found in *Peromyscus maniculatus* and *Microtus californicus* in the same locality.

39. **Hepatozoon* sp. KEYMER, 1964; *Tatera leucogaster* (83) Luangwa valley, **Zambia** (KEYMER, 1964, 1966).

KEYMER suggested this haemogregarine was *H. gerbilli* (3) first described from *T. indica* in **India**.

40. *Hepatozoon erhardovae* KRAMPITZ, 1964; *Clethrionomys glareolus* (67) **England** (JACOBS, 1953; BAKER et al., 1963); **Czechoslovakia** (ERHARDOVA, 1955; ČERNA, 1957); **France** (DOBY et al., 1964); **W. Germany** (KRAMPITZ, 1964); **Austria** (MAHNERT, 1972); **Sweden** (TADROS, unpublished); *Clethrionomys rutilus* (68) **W. Germany** (KRAMPITZ, 1964).

The report by DOBY et al. (1964) is unusual in that the haemogregarine was found as schizonts in sections of lung.

41. *Hepatozoon* sp. DASGUPTA, 1965; *Petaurista magnificus* (43) **Darjeeling, India**.

42. *Hepatozoon* sp. KEYMER, 1966; *Aethomys ?kaiseri* (104) Chitala area, **Malawi** (KEYMER, 1966); **Uganda** (MINTER, unpublished).

43. **Hepatozoon* spp. KEYMER, 1966; *Otomys kempi* (126) *Lophuromys flavopunctatus* (121) **Myika Plateau, Zambia**.

KEYMER (1966) found a single intra-erythrocytic haemogregarine in the blood of one *Otomys*, and a profuse schizogony in the myocardium, connective tissue, diaphragm, spleen and lungs of a second in the blood of which no gametocytes were found. Schizonts were also seen in the lungs and heart of a *Lophuromys* which once again had no parasites in the blood. The tissue forms may have been stages in the life-cycle of a parasite other than *Hepatozoon*.

44. *Hepatozoon* sp. KRAMPITZ, SACHS, SCHALLER & SCHINDLER, 1968; *Mastomys natalensis* (114) **Uganda**.

45. *Hepatozoon epsteini* KAKABANZE & ZASUKHIN, 1969; *Rattus* sp. (113) **Sukhumi, E. shore of Black Sea, U.S.S.R.**

From the description of this parasite, it is certainly different from *H. muris* (2), a widespread parasite of *Rattus* ssp.

46. *Hepatozoon* sp. KITCHINGS, DUNAWAY & STORY, 1970; *Sigmodon hispidis* (63) **U.S.A.**

This parasite came to light in a study of the blood of irradiated laboratory-bred rodents.

47. *Hepatozoon* sp. KILLICK-KENDRICK & BELLIER, 1971²; *Idiurus macrotis* (54) **Ivory Coast, West Cameroons**.

48. *Hepatozoon* sp. KILLICK-KENDRICK & BELLIER, 1971²; *Idiurus macrotis* (54) **Ivory Coast**.

This second, less common, haemogregarine of the pygmy flying squirrel has unusually long gametocytes (27.5–38.5 μm) and is perhaps closer to *Haemogregarina* than *Hepatozoon*.

² The haemogregarines of the pygmy flying squirrel will be described and named in a later paper of the present series.

49. *Hepatozoon* spp. MAHNERT, 1972; *Pitymys subterraneus* (71), *Microtus nivalis* (73) **Austria**.
MAHNERT (1972) also recorded *Hepatozoon* spp. in *M. agrestis* (72), *C. glareolus* (67) and *Apodemus* spp. (94) in **Austria**; they are here referred to *H. microti* (13), *H. erhardovae* (40), and *H. sylvatici* (15), respectively.
50. *Hepatozoon* sp. BRUCE-CHWATT & GIBSON (unpublished); *Hybomys trivirgatus* (103) **W. Nigeria**.
51. *Hepatozoon* sp. BRUCE-CHWATT & GIBSON (unpublished); *Praomys tullbergi* (116) **W. Nigeria**.
52. *Hepatozoon* sp. LAINSON (unpublished); *Holochilus brasiliensis* (62) **Brazil**.
53. *Hepatozoon* sp. LAINSON (unpublished); *Oryzomys capito* (55) **Brazil**.
54. *Hepatozoon* sp. LANDAU (unpublished); *Hybomys univittatus* (102) **Central African Republic**.
55. *Hepatozoon* sp. LANDAU (unpublished); *Xerus rutilus* (28) **Ethiopia**.
56. *Hepatozoon* sp. MARKUS (unpublished); *Xerus inauris* (29) **S. Africa**.

Plasmodiidae

Plasmodiidae contains the single genus of true malaria parasites, *Plasmodium* MARCHIAFAVA & CELLI, 1885. The species infecting rodents form part of the subgenus *Vinckeia* (GARNHAM, 1964). The two known in murine rodents of Africa are divided into subspecies recognised by differences in distribution and the morphology of the sporogonic and exoerythrocytic stages (LANDAU & KILLICK-KENDRICK, 1966; GARNHAM et al., 1967; BAFORT, 1968; LANDAU et al., 1968; 1970; KILLICK-KENDRICK, 1973). *P. berghei yoelii* LANDAU & KILLICK-KENDRICK, 1966, is here raised to a species, with subspecies *killicki* and *nigeriensis* transferred from species *berghei* to species *yoelii*. This gathers the lowland populations of the *berghei* group into one species which differs from *P. berghei* VINCKE & LIPS, 1948, by (i) the vertebrate and invertebrate hosts, (ii) the sizes of the mature oocysts, (iii) the lengths of the sporozoites, (iv) the rates of growth of the tissue stages, (v) electrophoretic mobilities of enzymes and (vi) differences in DNA (KILLICK-KENDRICK, in press; CARTER, 1973; CHANCE & WARHURST, 1973).

57. *Plasmodium berghei* VINCKE & LIPS, 1948; *Grammomys surdaster* (96) (VINCKE & LIPS, 1948; VINCKE, 1954); *Praomys jacksoni* (115), *Leggada bella* (120) (VINCKE, 1954), **Katanga Province, Congo-Kinshasa (Zaire)**.
58. *Plasmodium yoelii yoelii* LANDAU & KILLICK-KENDRICK, 1966; *Thamnomys rutilans* (95) **Central African Republic** (LANDAU & CHABAUD, 1965).
59. *Plasmodium yoelii killicki* LANDAU, MICHEL & ADAM, 1968; *Thamnomys rutilans* (95) **Congo-Brazzaville** (ADAM et al., 1966).
60. *Plasmodium yoelii nigeriensis* KILLICK-KENDRICK, 1973; *Thamnomys rutilans* (95) **W. Nigeria** (KILLICK-KENDRICK et al., 1968).
61. *Plasmodium vinckei vinckei* RODHAIN, 1952; *Grammomys surdaster* (?) (96) **Katanga Province, Congo-Kinshasa (Zaire)**.

P. v. vinckei has never been found in a rodent, and is known only by two isolations from the mosquito *Anopheles durenii millescampsii* (RODHAIN, 1952; BAFORT, 1967). Since *A. d. millescampsii* appears to feed exclusively on rodents (see GILLIES & DE MEILLON, 1968), there is no doubt that the natural vertebrate host is a silvatic rodent in the forest galleries of **Katanga**, and the most likely animal is *G. surdaster*.

62. *Plasmodium vinckei* ssp. BRUCE-CHWATT & GIBSON, 1955; *Praomys tullbergi* (116) (BRUCE-CHWATT & GIBSON, 1955); *Thamnomys rutilans* (95) (KILLICK-KENDRICK et al., 1968), **W. Nigeria.**

A third of the *T. rutilans* in this locality were found to be infected with *P. vinckei* ssp. whereas only one out of more than 1,000 *Praomys* was infected (KILLICK-KENDRICK, 1973). This suggests either that the single infected *Praomys* was a misidentified *Thamnomys*, or that the *Praomys* had a very rare accidental infection of a parasite of *Thamnomys*.

63. *Plasmodium vinckei chabaudi* LANDAU, 1965; *Thamnomys rutilans* (95) **Central African Republic** (LANDAU, 1965; LANDAU & CHABAUD, 1965).

This parasite was first named *P. chabaudi* but later placed as a subspecies of *P. vinckei* by BAFORT, (1968).

64. *Plasmodium vinckei lentum* LANDAU, MICHEL, ADAM & BOULARD, 1970; *Thamnomys rutilans* (95) **Congo-Brazzaville** (ADAM et al., 1966)

65. *Plasmodium atheruri* VAN DEN BERGHE, PEEL, CHARDÔME & LAMBRECHT, 1958; *Atherurus africanus* (139) **Cameroun** (LANGUILLON, 1957), **Irangi Forest, Congo-Kinshasa (Zaire)** (VAN DEN BERGHE et al., 1958), **Congo-Brazzaville** (LANDAU et al., 1969a).

66. *Plasmodium anomaluri* PRINGLE, 1960; *Anomalurus derbianus* (52) **Chemka, Tanzania.**

67. *Plasmodium booliati* SANDOSHAM, YAP & OMAR, 1965; *Petaurista petaurista* (44) **W. Malaysia.**

68. *Plasmodium watteni* LIEN & CROSS, 1968; *Petaurista petaurista grandis* (45) **Taiwan.**

69. *Plasmodium* sp. YAP, MUUL & LIM, 1970; *Petaurista elegans* (46) **W. Malaysia.**

70. *Plasmodium* spp. KILLICK-KENDRICK & BELLIER, 1971; *Anomalurus peli* (53), *A. derbianus* (52) **Ivory Coast.**

Two new malaria parasites of *A. peli* are described and named *P. landauae* and *P. pulmophilum* by KILLICK-KENDRICK (1973 a).

71. *Plasmodium* spp. YAP (unpublished); *Petinomys vordermanni* (47) *Hylopetes spadicus* (49) **W. Malaysia.**

Mr. YAP LOY FONG (personal communication) found light infections of undoubted malaria parasites in both these flying squirrels. Too few parasites were seen for an identification to be made.

Haemoproteidae

Haemoproteidae includes the genera *Hepatocystis* LEVADITI & SCHOEN 1932 emend. GARNHAM, 1948, and *Rayella* DASGUPTA, 1967. Among rodents, *Hepatocystis* is found exclusively in Asian squirrels. The commoner of the two species of *Hepatocystis* of these animals, *H. vassali* (LAVERAN, 1905b), is divided into four subspecies based upon geographical distribution and minor morphological differences of the gametocytes (GARNHAM, 1966).

Rayella DASGUPTA, 1967, was created to accommodate an *Hepatocystis*-like parasite of giant flying squirrels in parts of Asia. It differs from *Hepatocystis* by the morphology of the tissue stages (merocysts) which were described as small cystic schizonts occurring in groups in the liver. *Hepatocystis* is divided into species largely on the basis of the morphology of the asexual stages in the tissues (GARNHAM, 1966), and possibly the separation of *Rayella* solely on this character would not be generally accepted. Another difference, however, is the time

necessary for the exflagellation of the microgametes of *Rayella* (8 mins) (DASGUPTA & CHATTERJEE, 1969), which differs from the characteristically short time (< 3 mins) of *Hepatocystis*.

72. *Hepatocystis vassali vassali* (LAVERAN, 1905); *Callosciurus flavimanus griseimanus* (11) (VASSAL, 1905, 1907; LAVERAN, 1905b), *C. vittatus* (20) (VASSAL, 1907), *C. flavimanus* ssp. (12) (VAN PEENEN et al., 1968), *Callosciurus* sp. (21) (VASSAL, 1907) **Vietnam**; *Callosciurus finlaysoni* (14), *Tamiops maccllellandii kongensis* (24) (COATNEY et al., 1960) **Thailand**.
73. *Hepatocystis vassali ratufae* (DONOVAN, 1920); *Ratufa indica* (6) **India** (DONOVAN, 1920; MULLIGAN & SOMERVILLE, 1947); *R. bicolor gigantea* (5) **Thailand** (COATNEY et al., 1960); *R. macroura* (7) **Ceylon** (DISSANAIKE, 1963); *Ratufa bicolor* (8) *R. affinis* (9) (MUUL et al., 1970) *Ratufa* spp. (10) (WHARTON et al., 1963) **W. Malaysia**.
74. *Hepatocystis vassali malayensis* FIELD & EDESON, 1950; *Callosciurus notatus minutus* (18) *C. nigrovittatus* (19) (GREEN, 1934; MUUL et al., 1970); *C. caniceps* (15) *C. notatus* (17) *Sundasciurus tenuis* (22) (FIELD & EDESON, 1949, 1950; MUUL et al., 1970); *S. hippurus* (23) (MUUL et al., 1970); *Lariscus insignis* (26) (DUNN et al., 1968); *Callosciurus* sp. (21) (WHARTON et al., 1963) **W. Malaysia**; *C. prevostii* (16) London Zoo (quoted by COATNEY & ROUDABUSH, 1949).
 Reports of *Hepatocystis* in callosciurine tree squirrels of **West Malaysia** are here arbitrarily grouped under subspecies *malayensis* whether or not specific or subspecific identifications of the parasite were given in the original accounts. FIELD & EDESON (1949) mistakenly reported *Hepatocystis* in two W. Malaysian specimens of *L. insignis* (FIELD & EDESON, 1950); the report by DUNN et al. (1968) is the sole record of *Hepatocystis* in this rodent. The latter workers also reported *Hepatocystis* in a burrowing myomorph, *Rhizomys sumatrensis*, but this was a clerical error (YAP LOY FONG, personal communication). COATNEY & ROUDABUSH (1949) listed a malaria parasite *sensu lato* in "*Sciurus stramineus guayanus*" in London Zoo. It is probable that the parasite was *Hepatocystis*, but I know neither the modern name of the rodent nor its country of origin.
75. *Hepatocystis vassali yokogawai* WU, 1953; *Callosciurus flavimanus taiwanensis* (13) (WU, 1953; MANWELL & KUNTZ, 1966), *Tamiops maritimus maritimus* (25) (WU, 1953) **Taiwan**.
76. *Hepatocystis* sp. KILLICK-KENDRICK, GARNHAM & RAJAPAKSA, 1973; *Callosciurus nigrovittatus* (19) **Sabah, E. Malaysia**.
 This may be a new subspecies of *H. vassali* from **Borneo**.
77. *Hepatocystis* sp. YAP (unpublished); *Petaurista petaurista* (44) **W. Malaysia**.
 The merocysts of this parasite have not been seen. Since the host is a giant flying squirrel, it is possible that YAP's parasite is a new Malaysian species of *Rayella*.
78. *Rayella rayi* (TOKURA & WU, 1961); *Petaurista inornatus* (42) **Mukteswar, India** (RAY, 1949, 1960); *P. magnificus* (43) **Darjeeling, India** (DASGUPTA, 1965, 1967); *P. petaurista grandis* (45) **Taiwan** (TOKURA & WU, 1961; MANWELL & KUNTZ, 1966; LIEN & CROSS, 1968).
79. *Rayella hylopetei* DASGUPTA, PAL, CHATTERJEE & CHATTERJEE, 1971; *Hylopetes alboniger* (48) **Darjeeling, India**.

Babesiidae

Babesiidae includes the piroplasms of rodents, which are here all rather arbitrarily placed in the genus *Babesia* STARCOVICI, 1893. It seems certain that more than one genus is represented, but the differential criteria are far from clear. NEITZ (1956) listed ten synonyms of

Babesia which were given because of differences in the size, shape and method of division of the form in the red-cell. SHORTT (1962) pointed out that these morphological characters tended to overlap with one another, and NEITZ, SHORTT and others had no doubts that the group will have to be revised as soon as more life-cycles in the invertebrate host (ticks) become known. NEITZ (1965) suggested that the complement fixation test may prove to be a means of recognising species of *Babesia*, whereas GOURLAY et al. (1970) believed that disc electrophoresis of soluble proteins would prove to be a useful aid in identification.

Russian workers (CHEISSIN, 1965; KRYLOV, 1965) place some piroplasms in the genus *Nuttallia* on the basis of division into 4 in the red-cell, and an absence of transovarial transmission in the tick; this view is gaining support (NOWELL, 1969; McMILLAN & BROCKLESBY, 1971). Other piroplasms of rodents appear to be closely related to *Theileria*, dividing as schizonts (Koch's blue bodies) in the internal organs (see NEITZ, 1956). Examples are the parasites found by TSUR et al. (1960) in a gerbil of Israel, by VAN PEENEN & ATALLA (1963) in an Egyptian gerbil, and possibly the piroplasms described by FAY & RAUSCH (1969) from Alaskan voles. At the moment, it seems that the only way to achieve a semblance of order is to lump the piroplasms of rodents together in the genus *Babesia*, and await a revision of the whole group which will doubtless follow as more complete life-cycles become known.

The confusion extends to the higher taxa. In the present work, Piroplasma is considered as a class of the Sporozoa because of observations on the fine structure of piroplasms, which are now known to have organelles typical of the subphylum (see LEVINE, 1971). Earlier some workers (e.g. CHEISSIN, 1965) suggested piroplasms should be considered as blood-inhabiting amoebae and be classified in the super-class Sarcodina of the subphylum Sarcomastigophora, but this notion has now lost support.

LEVINE (1971) synonymizes a number of piroplasms of rodents, and suggests that the number of true species may be very small indeed. In the present work the names have largely been retained because it is feared that a sweeping synonymy in the absence of knowledge of life-cycles may lead to good species being doubted, or even being later overlooked.

In light infections in rodents, piroplasms are easily mistaken for malaria parasites. Both inhabit erythrocytes, and young rings of *Plasmodium* are similar to *Babesia*. The true schizogony of *Plasmodium* in the blood is, however, thought to be absent in *Babesia*, and although pigment is said to be produced by at least one piroplasm (MOLYNEUX & BAFORT, 1970), it is not visible, as in malaria parasites, with the light microscope.

80. *Babesia muris* (FANTHAM, 1905); *Rattus norvegicus* (107) England.
 This parasite was seen in three laboratory white rats (FANTHAM, 1905, 1906). Presumably the infection was acquired from ticks in the bedding of the cage, and the parasite may have been *Babesia microti*, the common piroplasm of British small mammals. If so, the name *muris* would have priority over *microti*.
81. *Babesia quadrigemina* (NICOLLE, 1907); *Ctenodactylus gundi* (50) Tunisia.
82. *Babesia avicularis* WENYON, 1909; *Lemniscomys barbarus* (100) Sudan.
83. *Babesia microti* (FRANÇA, 1912); *Microtus agrestis* (72) Portugal (FRANÇA, 1912); *Arvicola terrestris* (69) (COLES, 1914), *Apodemus sylvaticus* (93) (COLES, 1914; JACOBS, 1953; SHORTT & BLACKIE, 1965; YOUNG, quoted by COX, 1970). *Micromys minutus* (91) (YOUNG, quoted by COX, 1970) England; *Microtus agrestis* (72) (COLES, 1914; BAKER et al., 1963; SHORTT & BLACKIE, 1965; YOUNG, quoted by COX, 1970), *Clethrionomys glareolus* (67) (JACOBS, 1953; SHORTT & BLACKIE, 1965; NOWELL, 1969; YOUNG, quoted by COX, 1970) England; Austria (MAHNERT, 1972); *Microtus nivalis* (73) *Pitymys subterraneus* (71) Austria (MAHNERT, 1972); *Microtus pennsylvanicus* (78) Mass., U.S.A. (TYZZER, 1938) New York, U.S.A. (KIRNER et al., 1958); *Microtus californicus* (75) *Peromyscus californicus* (57) *Neotoma lepida* (64) California, U.S.A. (VAN PEENEN & DUNCAN, 1968).
 MAHNERT's (1972) unidentified piroplasms of Austrian rodents are here referred to *B. microti*. In a laboratory study on the course of infection in laboratory rodent of strains of this piroplasm from several English hosts, SHORTT & BLACKIE (1965) found no differences in infectivity or morphology. This suggests that piroplasms of small rodents in England, and possibly other parts of Europe are represented by one species, *B. microti*. However, the name *B. colesi* LEVINE, 1971 has recently been proposed for the piroplasm of *A. sylvaticus* in England. It was first named *Nuttallia muris* COLES, 1914, and later moved to *Babesia* by REICHENOW (1953). LEVINE saw that *Babesia muris* was a homonym of FANTHAM's (1905) piroplasm of the white rat and gave the new name to the parasite of *Apodemus*. I view *B. colesi* as a synonym of *B. microti*.
84. *Babesia decumani* (MACFIE, 1915); *Rattus norvegicus* (107) Ghana (MACFIE, 1915), Vietnam (CAPPONI et al., 1955); *R. bowersi* (109) *R. sabanus* (110) *R. musschenbroeki* (111) W. Malaysia (YAP & SANDOSHAM, 1963).
 CAPPONI et al. (1955) did not identify the piroplasm they found in Vietnam, but since it appears to have been morphologically indistinguishable from MACFIE's and was in the same host, the record is included here. *B. decumani* may be a synonym of *B. muris* (FANTHAM, 1905).
85. *Babesia* sp. BRUCE, HARVEY, HAMERTON, DAVEY & BRUCE, 1915; *Thryonomys swinderianus* (?) (140).
86. *Babesia rossica* (YAKIMOFF & SAPHRONOWITSCH, 1917); *Microtus* sp. (?) (79) Saratov Province, U.S.S.R.
 This was first described as *Theileria*, but there was no real evidence it belonged to this genus (WENYON, 1926). ZASUKHIN (1956) assigned it to *Gonderia*, again for reasons which are not clear.
87. *Babesia rigolleti* (LÉGER & BÉDIER, 1922); *Graphiurus murinus* (137) Senegal.
B. rigolleti was first named as a *Plasmodium*. WENYON (1926) noted the lack of pigment, and BRAY (1964) referred it to the genus *Babesia*.
88. *Babesia golundae* (LÉGER & BÉDIER, 1923); *Mylomys lowei* (97) Senegal.
89. *Babesia myoxi* (FRANCHINI, 1924); *Muscardinus avellanarius* (135) Italy.
90. *Babesia* sp. NAUCK, 1927; *Sciurus vulgaris* (2) China.
91. *Babesia kolzovi* (ZASUKHIN, 1930); *Citellus pygmaeus* (37) W. Kazakhstan, U.S.S.R. (ZASUKHIN, 1930, 1931); *Citellus fulvus* (34) U.S.S.R. (ZASUKHIN, 1936).
92. *Babesia eliomyysi* (GALLI-VALERIO, 1930); *Eliomys quercinus* (136) Switzerland.
93. *Babesia ratti* SCHWETZ & COLLART, 1930; *Arvicanthis niloticus* (99) Congo-Kinshasa (Zaire) (SCHWETZ & COLLART, 1930), Uganda (PEIRCE, 1972); *Mastomys natalensis* (114) Congo-Kinshasa (Zaire) (SCHWETZ & COLLART, 1930).
 SCHWETZ & COLLART thought this parasite was possibly the same as *B. avicularis* WENYON, 1909, and *B. decumani* (MACFIE, 1915). LEVINE (1971) and PEIRCE (1972) view the piroplasm of *Arvicanthis* as *B. avicularis*, but until a proper comparison is made of the piroplasms of *Arvicanthis* and *Lemniscomys* I think they are best left with separate names.

94. *Babesia citelli* BECKER & ROUDABUSH, 1934; *Citellus tridecemlineatus* (38) Iowa, U.S.A.
95. *Babesia gerbilli* (TIVLOV, 1934); *Rhombomys opimus* (89) U.S.S.R. (ZASUKHIN et al., 1934).
96. *Babesia volgensis* (ZASUKHIN, 1936); *Citellus fulvus* (34) W. Kazakhstan, U.S.S.R. A redescription of this parasite is given by ZASUKHIN (1956).
97. *Babesia* sp. TARTAKOVSKY (quoted by ZASUKHIN, 1936); (captive) *Citellus* sp. (40) Leningrad, U.S.S.R.
98. *Babesia cricetuli* (SPRINHOLZ-SCHMIDT, 1937); *Cricetulus furunculus* (66). U.S.S.R.
99. *Babesia jakimovi* (SPRINHOLZ-SCHMIDT, 1937); *Tamias sibiricus asiaticus* (41) Eastern U.S.S.R.
100. *Babesia tucohucoi* CARINI, 1941; *Ctenomys* sp. (138) Brazil.
101. *Babesia epsteini* (ZASUKHIN, 1947); *Citellus pygmaeus* (37) W. Kazakhstan, U.S.S.R.
102. *Babesia wrighti* TOMLINSON, SMITH & FOGG, 1948; *Citellus variegatus buckleyi* (39) Texas, U.S.A.
103. *Babesia lemniscomysi* (ROUSSELOT, 1949); *Lemniscomys striatus* (101) Congo-Brazzaville.
104. *Babesia rhombomys* (CELISCHTICHEV, 1950); *Rhombomys opimus* (89) W. Kazakhstan, U.S.S.R.
105. *Babesia rodhaini* VAN DEN BERGHE, VINCKE, CHARDÔME & VAN DEN BULCKE, 1950. *Grammomys surdaster* (96) Congo-Kinshasa (Zaire).
The type locality of *B. rodhaini* is Sungu on the River Lufufui, 40 km from Kamina (VAN DEN BERGHE et al., 1950). Strains from another locality, the River Kasapa, near Lumbumbashi (Elisabethville), were morphologically the same, but differed in infectivity to experimental rodents (RODHAIN & VINCKE, 1953).
106. *Babesia graingeri* HEISCH, 1952; *Euxerus erythropus fulvior* (31) Kenya.
107. *Babesia taterilli* (ROUSSELOT, 1953); *Taterillus gracilis* (84) Mali (ROUSSELOT, 1953), Haute Volta (LANDAU, unpublished).
108. *Babesia merionis* (ROUSSELOT, 1953); *Meriones tristrami* (87) Iran.
Intact and splenectomized white rats, splenectomized mice and intact hamsters were refractory to infection by the inoculation of blood.
109. *Babesia* sp. BRUCE-CHWATT & GIBSON, 1955; *Praomys tullbergi* (116) W. Nigeria.
110. *Babesia* sp. BRUCE-CHWATT & GIBSON, 1955; *Thryonomys swinderianus* (140) W. Nigeria.
According to BRAY (1964), the piroplasm in Nigerian *Thryonomys* is different from the one found in the same host in Liberia.
111. *Babesia danii* (TSUR, HADANI & PIPANO, 1960); *Meriones tristrami* (87) Israel (ADLER, 1930; TSUR et al., 1960; FELDMAN MUHSAM, 1962).
FELDMAN-MUHSAM (1962) named this parasite *Nuttalia adleri*, but before her paper appeared TSUR et al. (1960) had given the name *N. danii* which has priority. This piroplasm should perhaps be assigned to the genus *Theileria* rather than *Babesia* (see NETZ, 1956). TSUR et al. (1960) described "schizont-like" division stages, resembling Koch's blue bodies, in smears of internal organs, as well as division stages in the blood. BARNETT & BROCKLESBY (1969) considered it to be a link between the *Babesiidae* and *Theileriidae*.
112. *Babesia* sp. FRANSEN & GRUNDMANN, 1961; *Neotoma lepida* (64) Utah, U.S.A.
This may be the piroplasm of *N. lepida* recorded by VAN PEENEN & DUNCAN (1968) in California U.S.A. and identified by them as *B. microti*.
113. *Babesia* sp. VAN PEENEN & ATALLA, 1963; *Meriones libycus libycus* (86) Egypt.
As with *B. danii*, division stages of this parasite similar to Koch's blue bodies of *Theileria* spp. were seen in tissue smears of experimentally infected *Meriones*; they were found in smears of the kidney 18 days after inoculation. VAN PEENEN & ATALLA (1963) suggest that this piroplasm was *B. danii* adapted to a different host.
114. *Babesia* sp. VAN PEENEN & ATALLA, 1963; *Gerbillus campestris* (80) Egypt.
Although this piroplasm looked like the one of *M. libycus* from the same locality, *Meriones* was found to be refractory to infection. This report of two biologically distinct piroplasms of related hosts in a single locality, coupled with the records of *B. danii* (111) of *M. tristrami* in Israel, *B. tadjikistanica* (115) of *M. erythourus* in the U.S.S.R. and *B. taterilli* (107) of *T. gracilis* in Mali, suggests that there is a closely

related complex of species or subspecies of piroplasms in gerbillines. They warrant a comparative study.

115. *Babesia tadjhikistanica* (KRYLOV & ZANINA, 1963); *Meriones erythrourus* (85) **Tadjhikistan, U.S.S.R.**

This parasite was first named *Smithia tadjhikistanica*, but Russian workers now prefer to place it in the genus *Nuttallia* which in their view differs from *Babesia*, *Smithia* etc. by the absence of transovarial transmission in the arthropod host (CHEISSIN, 1965; KRYLOV, 1965).

BARNETT & BROCKLESBY (1969) suggested that this piroplasm of a Russian gerbil was probably the same as *Babesia danii* (111) of *Meriones tristrami* in **Israel**.

116. *Babesia bandicootia* MANWELL & KUNTZ, 1964; *Bandicota indica nemorivaga* (123) **Taiwan**.

117. *Babesia* sp. MANWELL & KUNTZ, 1964; *Rattus coxinga coxinga* (112) **Taiwan**.

118. *Babesia* sp. BRAY, 1964; *Thryonomys swinderianus* (140) **Liberia**.

119. *Babesia* sp. GUNDERS (BRAY, 1964); *Praomys tullbergi* (116) **Liberia**.

120. *Babesia* sp. VAN PEENEN & DUNCAN, 1968; *Citellus beecheyi* (33) **California, U.S.A.**

121. *Babesia* spp. FAY & RAUSCH, 1969; *Microtus oeconomus* (77) *M. pennsylvanicus* (78) *Clethrionomys rutilus* (68) **Alaska, U.S.A.**

FAY & RAUSCH found two quite different piroplasms in Alaskan voles which seemed to reproduce principally by schizogony in the tissues. One, from *M. oeconomus*, appeared seldom, if ever, to divide in red-cells and was not infective to *C. rutilus*.

122. *Babesia hylomyisci* BAFORT, TIMPERMAN & MOLYNEUX, 1970; *Hylomyscus stella* (118) **Katanga Province, Congo-Kinshasa (Zaire)**.

123. *Babesia meri* (GUNDERS, 1971); *Psammomys obesus* (88) **Israel**.

124. *Babesia* sp. (GUNDERS & SARFATTI, 1971); *Nesokia indica* (124) **Israel**.

125. *Babesia* sp. YAP, 1972; *Hylopetes spadiceus* (49) **W. Malaysia**.

126. *Babesia* sp. PEIRCE, 1972; *Praomys jacksoni* (115) **Kenya**.

127. *Babesia muratovi* nom. nov.; *Mus musculus* (119) **Tadjhikistan, U.S.S.R.**

MURATOV (1966) compared the morphology of this piroplasm of mice with that of *B. tadjhikistanica*, a parasite of jirds in the same locality, and found it was different; moreover, although mice were susceptible to the parasite from jirds, that of mice failed to infect *Meriones*. MURATOV (1966) named the mouse parasite *Nuttallia musculi* and LEVINE (1971) referred it to the genus *Babesia*. Unfortunately, because he was unable to compare it adequately with other piroplasms of rodents, MURATOV conditionally named the piroplasm of mice. By Article 15 of the International Code of Zoological Nomenclature (1964) the name *musculi* is not, therefore, available and the parasite is here re-named *Babesia muratovi* in honour of its discoverer.

128. *Babesia* sp. ADAM & LANDAU (unpublished); *Praomys jacksoni* (115) **Congo-Brazzaville**.

129. *Babesia* sp. ADAM & LANDAU (unpublished); *Thryonomys swinderianus* (140) **Congo-Brazzaville**.

130. *Babesia* sp. BRUCE-CHWATT & GIBSON (unpublished); *Cricetomys gambianus* (90) **Agege, W. Nigeria**.

131. *Babesia* sp. BRUCE-CHWATT & GIBSON (unpublished); *Stochomys longicaudatus* (117) **Agege, W. Nigeria**.

132. *Babesia* sp. LANDAU (unpublished); *Hybomys univittatus* (102) **Central African Republic**.

133. *Babesia* sp. LANDAU (unpublished); *Praomys jacksoni* (115) **Central African Republic**.

The unnamed piroplasms of *Praomys* in Nigeria (109), Liberia (119), Brazzaville (128), Kenya (126) and the Central African Republic may be the same.

Dactylosomidae

Anthemosoma was created to accommodate an unusual parasite of the spiny mouse (*Acomys*). When first encountered it was thought to be *Babesia*, but it was seen to undergo a quite different kind of multi-

plication in the erythrocytes of the host similar to the schizogony of *Plasmodium*; pigment was, however, completely absent. In parasitaemias heightened by splenectomy, dimorphic forms thought to be gametocytes were found, and a resemblance to the dactylosomes of fishes and amphibia was recognised. The new genus, *Anthemiosoma* LANDAU, BOULARD & HOUIN, 1969, was therefore placed in the family Dactylosomidae (Piroplasmae; Piroplasmida). LEVINE (1971) felt this position was wrong and that *Anthemiosoma* was perhaps closer to the malaria parasites than the piroplasms. From the fine-structure, however, *Anthemiosoma* seems more to resemble piroplasms than *Plasmodium* (VIVIER & PETITPREZ, 1969), and it is perhaps best to leave *Anthemiosoma* in Dactylosomidae until its life-cycle is known.

134. *Anthemiosoma garnhami* LANDAU, BOULARD & HOUIN, 1969; *Acomys percivali* (122) Omo Valley, Ethiopia.

Index of Rodents which are Hosts of Blood-Inhabiting Sporozoa

The numbers after the names of the parasites refer to the checklist in which the identity of some of the parasites is discussed, and the localities and sources are given. As in the checklist, an asterisk before the name of a haemogregarine indicates that the host-cell is an erythrocyte. In the higher taxa of rodents I have followed the classification of SIMPSON (1945) modified by WOOD (1955).

Sciuromorpha

Fam. Sciuridae (squirrels)

Subfam. Sciurinae (ground and tree squirrels)

Tribe Sciurini (European and American tree squirrels)

1. *Sciurus carolinensis* (grey squirrel)

Hepatozoon griseisciuri (34)

2. *Sciurus vulgaris* (red squirrel)

Hepatozoon sciuri (14)

Babesia sp. (90)

3. *Sciurus niger* (fox squirrel)

Hepatozoon sp. (35)

Tribe Funambulini (African tree squirrels and allied Asian genera)

4. *Funambulus pennanti* (palm squirrel or 5-striped Indian squirrel)

Hepatozoon funambuli (4)

Tribe Ratufini

5. *Ratufa bicolor gigantea* (giant squirrel)

Hepatocystis vassali ratufae (73)

6. *Ratufa indica* (Indian giant squirrel or Malabar squirrel)

Hepatocystis vassali ratufae (73)

7. *Ratufa macroura* (grizzled giant squirrel)

Hepatocystis vassali ratufae (73)

8. *Ratufa bicolor* (black giant squirrel)
Hepatocystis vassali ratufae (73)
9. *Ratufa affinis* (white-thighed giant squirrel)
Hepatocystis vassali ratufae (73)
10. *Ratufa* spp.
Hepatocystis ratufae (73)

Tribe Callosciurini (Oriental tree squirrels)

MOORE & TATE's (1965) detailed study of museum material of diurnal squirrels of the Indian and Indo-Chinese sub-regions gives by far the best guide to this difficult tribe, and although the composition of their species differs from earlier concepts, they group the squirrels in a logical way producing order from chaos.

The largest genus of the tribe is *Callosciurus*, in which ELLERMAN (1940) recognises 320 forms. For the Indo-Chinese subregion, MOORE & TATE list 59, and for the Malaysian sub-region MEDWAY (1969) gives 26. The range of the genus does not include the Indian sub-region, and *Callosciurus* is not found west of the Garo-Rajmahal Gap. In the Indo-Chinese and Malaysian subregions, the great rivers form the boundaries of the ranges of many of the subspecies.

According to MOORE & TATE, in the Indo-Chinese subregion there are 8 species with one Artenkreis of 4 allopatric species (*erythraeus*, *ferrugineus*, *flavimanus* and *finlaysoni*) spread throughout the region, and a second (*pygerythrus*, *phayrei*, *caniceps* and *inornatus*) which is less widespread and largely sympatric with the first. For the Malaysian subregion, MOORE & TATE list only 5 species, *prevostii*, *notatus*, *nigrovittatus*, *albescens* and *melanogaster*. MEDWAY (1969) gives three of these, *prevostii*, *notatus* and *nigrovittatus*, but also lists *flavimanus* and *caniceps* which MOORE & TATE recognise in the Indo-Chinese but not in the Malaysian subregion. This lack of agreement, coupled with a very large number of subspecific names, makes it impossible confidently to assign some old records of *Hepatocystis* in Asian squirrels to hosts with current modern names.

11. *Callosciurus flavimanus griseimanus*
Hepatocystis vassali vassali (72)

LAVERAN (1905b) and VASSAL (1905, 1907) called this squirrel *Sciurus griseimanus*, now a synonym of *C. f. griseimanus* (MOORE & TATE, 1965; ELLERMAN & MORRISON-SCOTT, 1966).

12. *Callosciurus flavimanus* ssp.
Hepatocystis vassali vassali (72)

13. *Callosciurus flavimanus taiwanensis*
Hepatocystis vassali yokogawai (75)

MOORE & TATE (1965) recognise 19 subspecies of *C. flavimanus* (the belly-banded squirrel) distributed throughout the Indo-Chinese subregion east of the Sittang and Irrawaddy rivers, except Thailand, Cambodia and part of Laos (along the Mekong River) where *C. findlaysoni* occurs.

WU (1953) and MANWELL & KUNTZ (1966) record *Hepatocystis* in several squirrels in Taiwan which they identified as *C. erythraeus* and subspecies *roberti*, *centralis* and *taiwanensis*. MOORE & TATE, however, consider the range of *C. erythraeus* to be limited to west of the Irrawaddy and its tributary the river Nmai. They view *taiwanensis* as a subspecies of *flavimanus*, and list *centralis* and *roberti* as synonyms of subspecies *taiwanensis*.

14. *Callosciurus finlaysoni* (Siamese squirrel)
Hepatocystis vassali vassali (72)

Although MOORE & TATE (1965) accept *C. finlaysoni* as a good species, they do so only provisionally, and with some serious reservations. They list 15 subspecies distributed in Thailand, Cambodia and along the Mekong river in Laos. The record above is from Thailand, and the squirrel was thought to be close to the subspecies *boucourti* (COATNEY et al., 1960).

15. *Callosciurus caniceps* (grey-bellied squirrel)
Hepatocystis vassali malayensis (74)
16. *Callosciurus prevostii* (white-striped squirrel)
Hepatocystis vassali malayensis (74)
17. *Callosciurus notatus* (common red-bellied squirrel)
Hepatocystis vassali malayensis (74)
18. *Callosciurus notatus miniatus*
Hepatocystis vassali malayensis (74)

In this early record (GREEN, 1934) the host was given as *Callosciurus vittatus miniatus*.

19. *Callosciurus nigrovittatus* (black-banded squirrel)
Hepatocystis vassali malayensis (74)
Hepatocystis sp. (76)
20. *Callosciurus vittatus*
Hepatocystis vassali vassali (72)

This record, from Indo-China, is from a rodent not listed for the subregion by MOORE & TATE; it is not possible now to be sure of the host's identity.

21. *Callosciurus* sp.
Hepatocystis vassali vassali (72)
Hepatocystis vassali malayensis (74)

In the first of these records (VASSAL, 1907) the host was called *Sciurus* sp. The report was from Vietnam, and the animal would now be known as *Callosciurus*.

22. *Sundasciurus tenuis* (slender little squirrel)
Hepatocystis vassali malayensis (74)
23. *Sundasciurus hippurus* (horse-tailed squirrel)
Hepatocystis vassali malayensis (74)
24. *Tamiops maccllellandii kongensis* (striped tree squirrel)
Hepatocystis vassali vassali (72)
25. *Tamiops maritimus maritimus*
Hepatocystis vassali yokogawai (75)

In this report (WU, 1953) the host was given as "*Tamiops macellandi formosanus*". This is presumably the same as *Sciurus maccllellandii formosanus*, listed by MOORE & TATE (1965) as a synonym of *T. m. maritimus*.

26. *Lariscus insignis* (striped ground squirrel)
Hepatocystis vassali malayensis (74)
Tribe Xerini (African ground squirrels)
27. *Atlantoxerus getulus* (Barbary ground squirrel)
Hepatozoon getulum (18)
28. *Xerus rutilus*
Hepatozoon sp. (55)
29. *Xerus inauris*
Hepatozoon sp. (56)
30. *Euxerus erythropus* (red-legged ground squirrel)
Hepatozoon sp. (19)
31. *Euxerus erythropus fulvior*
Babesia graingeri (106)

Unlike a number of early workers, ROSEVEAR (1969) considers *Euxerus* to be separate from *Xerus*; he believes *fulvior* to be possibly a valid race of *X. microdon*, a synonym of *Euxerus erythropus*.

Tribe *Xerini incertae sedis*

32. *Spermophilopsis leptodactylus* (long-tailed ground squirrel)
Hepatozoon sp. (31)
- Tribe *Marmotini* (northern ground squirrels)
33. *Citellus beecheyi* (gopher)
Hepatozoon citellicolum (6)
Babesia sp. (120)
34. *Citellus fulvus* (large-toothed suslik)
Babesia kolzovi (91)
Babesia volgensis (96)
35. *Citellus guttatus* (ground squirrel)
Hepatozoon mereschkowskii (9)
36. *Citellus musicus* (ground squirrel)
Heptazon mereschkowskii (9)
37. *Citellus pygmaeus* (little suslik)
Babesia kolzovi (91)
Babesia epsteini (101)
38. *Citellus tridecemlineatus*
Babesia citelli (94)
39. *Citellus variegatus buckleyi* (black-backed rock-squirrel)
Babesia wrighti (102)
40. *Citellus* sp.
Babesia sp. (97)
41. *Tamias sibiricus asiaticus* (Siberian chipmunk)
Babesia jakimovi (99)

ZASUKHIN (1956) listed the host as *Eutamias asiaticus orientalis*. ELLERMAN & MORRISON-SCOTT (1966) give *Eutamias* as a subgenus of *Tamias*. They consider only one species, *T. (E.) sibiricus*, to be present in the U.S.S.R. and from their synonymy the host is assumed to be the subspecies *asiaticus*.

Subfam. *Petauristinae* (flying squirrels)

42. *Petaurista inornatus* (flying squirrel)
Rayella rayi (78)
43. *Petaurista magnificus* (Himalayan flying squirrel)
Heptazon sp. (41)
Rayella rayi (78)
44. *Petaurista petaurista* (giant flying squirrel)
Heptazon sp. (20)
Plasmodium booliati (67)
Hepatocystis sp. (77)
45. *Petaurista petaurista grandis*
Plasmodium watteni (68)
Rayella rayi (78)
46. *Petaurista elegans* (spotted giant flying squirrel)
Plasmodium sp. (69)
47. *Petinomys vordermanni* (black-winged flying squirrel)
Plasmodium sp. (71)
48. *Hylopetes alboniger* (particoloured flying squirrel)
Rayella hylopetei (79)
49. *Hylopetes spadiceus* (dark-tailed flying squirrel)
Plasmodium sp. (71)
Babesia sp. (125)

Sciuromorpha incertae sedis

Fam. Ctenodactylidae (gundis)

50. *Ctenodactylus gundi* (gundi)
Babesia quadrigemina (81)

51. *Pectinator spekei* (?)
Hepatozoon plicatum (11)

The host of *H. plicatum* in the Somali Republic was identified as a marmot (*Arctomys* [= *Marmota*] *marmota*), a rodent which is absent from Africa. BRUMPT (1946) suggested that the host was perhaps a hyrax mistaken for a rodent, a plausible idea since Italians in Africa call the hyrax "marmotta". But ROSEVEAR has pointed out to me that, in spite of its smaller size, another animal likely to have been confused with a marmot is the gundi *Pectinator*. This ctenodactylid is known only from the Somali peninsula (ELLERMAN, 1940) and like the marmot, lives in companies in rocky terrain. Only the re-discovery of the parasite will settle which animal was the host.

Theridomyomorpha

Fam. Anomaluridae (African scaly-tailed flying squirrels)

Subfam. Anomalurinae

52. *Anomalurus derbianus*
Plasmodium anomaluri (66)
Plasmodium landauae (70)
Plasmodium pulmophilum (70)

For more than a century, this animal was known as *A. fraseri*; the neglected name *derbianus* was then shown by ELLERMAN et al. (1953) to have priority over *fraseri* (see ROSEVEAR, 1969).

53. *Anomalurus peli*
Plasmodium spp. (70)

Subfam. Zenkerellinae

54. *Idiurus macrotis* (pygmy flying squirrel)
Hepatozoon sp. (47)
Hepatozoon sp. (48)

Myomorpha

Fam. Cricetidae

Subfam. Cricetinae

Tribe Hespermyini (New World mice)

55. *Oryzomys capito* (rice rat)
Hepatozoon sp. (53)
56. *Peromyscus boylii* (Boyle's white-footed mouse)
Hepatozoon sp. (38)
57. *Peromyscus californicus* (deer mouse)
Babesia microti (83)
58. *Peromyscus maniculatus* (Gambel's white-footed mouse)
Hepatozoon leptosoma (36)
59. *Peromyscus truei* (Gilbert's white-footed mouse)
Hepatozoon sp. (38)
60. *Akodon fuliginosus* (vole mouse)
Hepatozoon akodoni (16)
61. *Graomys medius*
Hepatozoon graomysi (28)

62. *Holochilus brasiliensis*

Hepatozoon sp. (52)

63. *Sigmodon hispidis* (cotton rat)

Hepatozoon sp. (46)

64. *Neotoma lepida* (wood rat)

Babesia microti (83)

Babesia sp. (112)

Tribe Cricetini (hamsters)

65. *Cricetus cricetus*

Hepatozoon criceti (8)

C. frumentarius, the name of the host of *H. criceti* in the original record, is a synonym of *C. cricetus* (ELLERMAN, 1941).

66. *Cricetulus furunculus*

Babesia cricetuli (98)

Tribe Microtini (voles)

67. *Clethrionomys glareolus* (bank vole)

Hepatozoon erhardovae (40)

Babesia microti (83)

68. *Clethrionomys rutilus*

Hepatozoon erhardovae (40)

Babesia sp. (121)

KRAMPITZ (1964) found *H. erhardovae* in W. Germany, a country which VAN DEN BRINK (1972) considers outside the range of *C. rutilus*.

69. *Arvicola terrestris* (water vole)

Hepatozoon sp. (32)

Babesia microti (83)

The piroplasm was found in England where this vole may be conspecific with *A. amphibius*, the northern European form (VAN DEN BRINK, 1972).

70. *Pitymys savii* (pine mouse)

Hepatozoon pitymysi (17)

71. *Pitymys subterraneus*

Hepatozoon sp. (49)

Babesia microti (83)

72. *Microtus agrestis* (short-tailed field vole)

Hepatozoon microti (13)

Babesia microti (83)

The piroplasm was first recorded from *M. incertus* from Portugal. This rodent is now considered to be a subspecies of *M. arvalis* restricted to Switzerland (ELLERMAN & MORRISON-SCOTT, 1966), or a synonym of *M. arvalis* which is absent from Portugal (VAN DEN BRINK, 1972). The Portuguese vole most similar to *M. arvalis* is *M. agrestis*, and the type host of *B. microti* is therefore referred to this species.

73. *Microtus nivalis*

Hepatozoon sp. (49)

Babesia microti (83)

74. *Microtus arvalis*

Hepatozoon lavieri (29)

Another species of *Hepatozoon*, *H. arvalis* (10), was reported from an Ethiopian rodent wrongly identified as *M. arvalis* (MARTOGLIO, 1913). The true identity of the host will never now be known with certainty, but it was possibly *Arvicanthis niloticus* (see BRUMPT, 1946).

75. *Microtus californicus*

Hepatozoon sp. (37)

Babesia microti (83)

76. *Microtus montebelli* (?)*Hepatozoon arvicolae* (25)

The host of this parasite found by MIYAIRI (1932) in Japan was given as *Arvicola hatengumi*. *Arvicola* is absent from Japan (ELLERMAN, 1941), and no mention of the specific epithet *hatengumi* appears in ELLERMAN'S comprehensive lists. It seems likely that the host was *M. montebelli*, the only Japanese field vole ELLERMAN gives.

77. *Microtus oeconomus* (root vole or northern vole)*Hepatozoon* sp. (33)*Babesia* sp. (121)

There are doubts about the identity of *M. oeconomus* (VAN DEN BRINK, 1972).

78. *Microtus pennsylvanicus**Hepatozoon* sp. (23)*Babesia microti* (83)*Babesia* sp. (121)79. *Microtus* sp. (?)*Hepatozoon microti* (13)*Babesia rossica* (86)

The hosts were described as field voles (YAKIMOFF & SAPHRONOWITSCH, 1917; DUBININ, 1953).

Subfam. Gerbillinae (gerbils, jirds, sand-rats, antelope rats)

80. *Gerbillus campestris**Babesia* sp. (114)81. *Tatera indica* (Indian gerbil)**Hepatozoon gerbilli* (3)

Gerbillus indicus, the host in the original report (CHRISTOPHERS, 1905), is now known as *Tatera indica*.

82. *Tatera indica ceylonica***Hepatozoon gerbilli* (3)83. *Tatera leucogaster***Hepatozoon* sp. (39)

KEYMER (1964, 1966) referred to the host as *Tatera afra*, but the record is from Zambia, which is outside the range of this species (DAVIS, 1966). At my request, Dr. G. B. CORBET of the British Museum (Natural History), London, kindly re-examined KEYMER'S deposited specimens, and they were then identified as *T. leucogaster*.

84. *Taterillus gracilis* (bushy-tailed gerbil)*Babesia taterilli* (107)

ROUSSELOT (1953) identified the type host of this parasite from Mali as *Tatera emini*, a rodent which is not found in West Africa. The gerbil most likely to have been collected in Mali is *Taterillus gracilis* (see ROSEVEAR, 1969), which LANDAU (unpublished) found infected with a morphologically similar piroplasm in Haute Volta.

85. *Meriones erythrourus* (jird)*Hepatozoon* sp. (30)*Babesia tadjikistanica* (115)

LATYSHEV (1949) called the host of the haemogregarine *M. libycus*, a predominantly N. African species with many forms. Since the report was from the U.S.S.R., it seems better to assign the host to *M. erythrourus*, a closely related rodent with a wide distribution in that country. The group is, however, difficult and the authorities give no clear guide; possibly *erythrourus* and *libycus* are distinct, although it has been suggested that *erythrourus* and its races may represent a subspecies of *libycus* (ELLERMAN, 1940).

86. *Meriones libycus libycus*
Babesia sp. (113)
87. *Meriones tristrami*
Babesia merionis (108)
Babesia danii (111)
88. *Psammomys obesus*
Babesia meri (123)
89. *Rhombomys opimus* (great gerbil)
 **Hepatozoon gerbilli* (3)
Babesia gerbilli (95)
Babesia rhombomys (104)

Subfam. Cricetomyinae

PETTER (1964) removed *Cricetomys* from the Muridae and created this subfamily of Cricetidae to accommodate the Gambian pouched rat.

90. *Cricetomys gambianus* (giant rat or Gambian pouched rat)
 **Hepatozoon cricetomysi* (26)
Babesia sp. (130)

Fam. Muridae

Subfam. Murinae (Old World rats and mice)

91. *Micromys minutus* (harvest mouse)
Babesia microti (83)
92. *Apodemus flavicollis* (yellow-necked mouse)
Hepatozoon sylvatici (15)
93. *Apodemus sylvaticus* (long-tailed field mouse)
Hepatozoon sylvatici (15)
Babesia microti (83)
94. *Apodemus* spp.
Hepatozoon sylvatici (15)
95. *Thamnomys rutilans* (shining thicket-rat)
Plasmodium yoelii yoelii (58)
Plasmodium yoelii killicki (59)
Plasmodium yoelii nigeriensis (60)
Plasmodium vinckei chabaudi (63)
Plasmodium vinckei lentum (64)
Plasmodium vinckei ssp. (62)
96. *Grammomys surdaster* (thicket-rat)
Plasmodium berghei (57)
Plasmodium vinckei vinckei (?) (61)
Babesia rodhaini (105)

The systematics of the thicket-rats present a number of problems which some workers solve by lumping them together in the single genus *Thamnomys*, sometimes divided into subgenera (e.g. DAVIS, 1965). ROSEVEAR (1969), however, suggests that 3 or 4 closely related genera of thicket-rats will eventually be recognised. He views *Grammomys* as separate from *Thamnomys* on the basis of (i) the absence of "gutter-hairs" found, for example, in the pelage of *Thamnomys rutilans*, (ii) "indisputable differences" in cuspidation and (iii) differences in the crania (see also GENEST-VILLARD, 1972).

97. *Mylomys lowei* (western 3-toed grass rat)
Babesia golundae (88)

The host of *B. golundae* from Senegal was given as *Golunda campanae*. This genus is Indian (ELLERMAN & MORRISON-SCOTT, 1966), and it seems likely that the infected rodent was an African groove-toothed swamp rat which was confused with *Pelomys campanae*. Although modern authorities are not in agreement, *Pelomys* is generally considered to be absent from West Africa where closely

related forms are now placed in *Mylomys* represented in that part of the continent by the single species *M. lowei* (see ROSEVEAR, 1969). This is, therefore, the probably identity of the host of *B. golundae*. An objection to this identification is the lack of reports of *Mylomys* in Senegal, but determined trapping in the nearby Ivory Coast by BELLIER has shown *M. lowei* to be common in that country (ROSEVEAR, 1969), and it is likely that *Mylomys* occurs in Senegal.

98. *Mylomys dybowskii* (eastern 3-toed grass rat)

Hepatozoon sp. (7)

The host of this parasite was called *Pseudomys cunninghami*. This is an Australasian genus (SIMPSON, 1945), and the rodent was probably *Mylomys cunninghamei*, now considered by ROSEVEAR (1969) to be a synonym of *M. dybowskii*.

99. *Arvicanthis niloticus* (harsh-furred rat)

Hepatozoon arvalis (?) (10)

Hepatozoon arvicanthis (21)

Babesia ratti (93)

MARTOGLIO's (1913) record of *Hepatozoon arvalis* (10) in a rodent in Ethiopia, mistaken for *Microtus arvalis*, was possibly from a misidentified *Arvicanthis* (see BRUMPT, 1946).

The host of *H. arvicanthis* is referred from *A. abyssinicus rubescens* to *A. niloticus* which ROSEVEAR (1969) suggests is the only species in the genus. ELLERMAN (1941) also considered there was little essential difference between the described species of *Arvicanthis*.

100. *Lemniscomys barbarus*

Babesia avicularis (82)

WENYON (1909) reported *B. avicularis* from a Sudanese rodent "*Avicularis zebrae*", later corrected to *Arvicanthis zebra* (WENYON, 1926). ELLERMAN (1941) does not list *zebra* as a form of *Arvicanthis*, and Wenyon's rodent was presumably *Lemniscomys barbarus zebra*. *Lemniscomys* is closely allied to *Arvicanthis*, but their separate identities were not recognized until the name *Lemniscomys* was resurrected in 1916 (ROSEVEAR, 1969). As two forms of *L. barbarus* other than *zebra* are known from the Sudan, the record is listed here with the subspecies undetermined.

101. *Lemniscomys striatus*

Babesia lemniscomysi (103)

102. *Hybomys univittatus* (one-striped rat)

Hepatozoon sp. (54)

Babesia sp. (132)

103. *Hybomys trivirgatus* (three-striped rat)

Hepatozoon sp. (50)

104. *Aethomys ?kaiseri*

Hepatozoon sp. (42)

There are about 16 forms of *A. kaiseri* among which there are possibly two species; they are not yet sorted out satisfactorily (DAVIS, 1965).

105. *Rattus assimilis* (allied rat)

Hepatozoon muris (2)

106. *Rattus conatus* (dusky field rat)

Hepatozoon muris (2)

107. *Rattus norvegicus* (brown rat; laboratory rat)

Hepatozoon muris (2)

Babesia muris (80)

Babesia decumani (84)

108. *Rattus rattus* (black rat)

Hepatozoon muris (2)

109. *Rattus bowersi*
Babesia decumani (84)
110. *Rattus sabanus* (giant long-tailed rat)
Babesia decumani (84)
111. *Rattus musschenbroeki* (little spiny rat)
Babesia decumani (84)
112. *Rattus coxinga coxinga*
Babesia sp. (117)
113. *Rattus* sp. ("grey rats")
Hepatozoon epsteini (45)
114. *Mastomys natalensis* (multi-mammate rat)
Hepatozoon sp. (44)
Babesia rattii (93)

The host of the piroplasm was given as *Mastomys ugandae*. This was a subspecies of *M. coucha* (ELLERMAN, 1941) a rodent which is now known as either *Mastomys natalensis* (e.g. ROSEVEAR, 1969) or *Praomys natalensis* (e.g. DAVIS, 1965).

115. *Praomys jacksoni*
Plasmodium berghei (57)
Babesia sp. (126, 128, 133)
116. *Praomys tullbergi*
Hepatozoon sp. (51)
Plasmodium vinckei ssp. (62)
Babesia sp. (109, 119)

Praomys provides some of the most difficult problems of taxonomy of any of the African Muridae, rivalled only by *Mastomys*. ROSEVEAR (1969) gives an up-to-date account of the difficulties from which it may be concluded that *Praomys* and *Mastomys* are likely to undergo extensive revision as new taxonomic procedures evolve.

117. *Stochomys longicaudatus*
Babesia sp. (131)
118. *Hylomyscus stella*
Babesia hylomysci (122)
119. *Mus musculus* (house mouse)
Hepatozoon musculi (5)
Babesia muratovi (127)

An unnamed piroplasm was recorded by BRUCE et al. (1911) in a white laboratory mouse (*Mus musculus*) in unusual circumstances. Mice were being used for the maintenance of a strain of spirochaete isolated from the blood of a bushbuck. Seven days after an inoculation of infected mouse blood, a recipient mouse was found to be infected with the spirochaete and a piroplasm. The piroplasm was seen on four successive days and then disappeared. Possibly it was a parasite of the bushbuck and the concomitant infection with the spirochaete may have enabled it to gain a temporary foothold in an abnormal host.

120. *Leggada bella* (pygmy mouse)
Plasmodium berghei (57)
121. *Lophuromys flavopunctatus*
Hepatozoon sp. (43)
122. *Acomys percivali* (spiny mouse)
Anthemosoma garnhami (134)
123. *Bandicota indica nemorivaga* (Indian bandicoot rat)
Babesia bandicootia (116)
124. *Nesokia indica*
Babesia sp. (124)

Subfam. Dendromurinae (African tree mice)

125. *Dendromus ?insignis*

**Hepatozoon dendromusi* (27)

Subfam. Otomyinae

126. *Otomys kempfi*

**Hepatozoon* sp. (43)

Fam. Dipodidae (jerboas)

Subfam. Dipodinae

A record by RODHAIN et al. (1913) of *Hepatozoon* sp. (12) in the erythrocytes of a dipodine ("*Jaculus ?johnstoni*") from Sankisia in the Republic of Zaïre (the then Belgian Congo) must have been from a wrongly identified host. The distribution of *Jaculus* does not extend below the Sahara Desert (OGNEV, 1948), and it is difficult now to be sure which was the rodent examined. It might have been a gerbil mistaken for a jerboa. Unlike the haemogregarines of almost all other myomorphs, those of both jerboas and gerbils are in erythrocytes, not leucocytes.

127. *Dipus sagitta* (rough-legged or 3-toed jerboa)

**Hepatozoon alactagae* (24)

Dipus sowerbyi, the host given in the report by JETTMAR (1932) (see also ZASUKHIN, 1936) is listed by ELLERMAN & MORRISON-SCOTT (1966) as a subspecies of *D. sagitta*.

128. *Jaculus gordonii*

**Hepatozoon balfouri* (1)

129. *Jaculus orientalis* (greater Egyptian jerboa)

**Hepatozoon balfouri* (1)

130. *Jaculus jaculus* (lesser Egyptian jerboa)

**Hepatozoon balfouri* (1)

131. *Allactaga major* (great jerboa)

**Hepatozoon alactagae* (24)

ZASUKHIN's (1936) host, *Alactaga jaculus*, is considered by ELLERMAN & MORRISON-SCOTT (1966) to be *Allactaga major*.

132. *Allactaga sibirica* (5-toed jerboa)

**Hepatozoon alactagae* (24)

JETTMAR (1932) called the host *Alactagulus mongolica*, which ELLERMAN & MORRISON-SCOTT (1966) give as a synonym of *Allactaga sibirica*. ZASUKHIN (1936), in quoting JETTMAR's record, used the name *Alactaga mongolica* in text, and *Jaculus mongolicus* in a table of hosts.

133. *Alactagulus pumilio* (little earth hare)

**Hepatozoon alactagae* (24)

A. acotion of the original report (ZASUKHIN, 1931) is considered to be a synonym of *A. pumilio* by ELLERMAN & MORRISON-SCOTT (1966) but not by OGNEV (1948) who lists *pumilio* as a synonym of *pygmaeus*.

134. *Stylodipus telum* (thick-tailed 3-toed jerboa)

**Hepatozoon alactagae* (24)

Stylodipus is called *Sciropoda* BRANDT, 1844 by Russian workers. Reasons for not using this name are given by ELLERMAN & MORRISON-SCOTT (1966, pp. 536–537).

Myomorpha incertae sedis

Fam. Gliridae

Subfam. Glirinae (dormice)

135. *Muscardinus avellanarius* (common dormouse)

Babesia myoxi (89)

136. *Eliomys quercinus*

Babesia eliomyi (92)

Hepatozoon lusitanicum (22)

The host of the haemogregarine was given as *Eliomys lusitanicum*, now a subspecies of *E. quercinus* (ELLERMAN, 1941).

Subfam. Graphiurinae (African dormice)

137. *Graphiurus murinus*

Babesia rigolleti (87)

BRAY (1964) thought that *G. murinus* was absent from West Africa and that the host of this piroplasm was possibly *G. hueti*. This is, however, improbable since *G. murinus* (= *Myoxus murinus*) is, in fact, found in West Africa (ROSEVEAR, 1969) and is unlikely to be confused with *G. hueti*, a large, very distinctive dormouse.

Caviomorpha

Fam. Ctenomyidae

138. *Ctenomys* sp. (tucu-tucu)

Babesia tucotucoi (100)

Fam. Caviidae (guinea pigs or cavies)

Subfam. Cavinae

There appear to be no true records of protozoa in the blood-cells of guinea-pigs. *Theileria caviae* CORRÊA, 1966 of *Cavia porcellus* of Brazil was later shown to be *Histoplasma capsulatum* by CORRÊA & PACHECO, 1967. MACFIE (1914) described two intra-erythrocytic "parasites" from laboratory-bred guinea-pigs in Nigeria. One, which MACFIE called *Paraplasma flavigellum*, was shown not to be a protozoon (WENYON & LOW, 1914), but the illustrations in MACFIE's paper suggest that the other, *Paraplasma cobayae*, was possibly a piroplasm.

Hystricomorpha

Fam. Hystricidae (Old World porcupines)

Subfam. Atherurinae (brush-tailed porcupines)

139. *Atherurus africanus* (brush-tailed porcupine)

Plasmodium atheruri (65)

Fam. Thryonomyidae

140. *Thryonomys swinderianus* (cane rat or cutting grass)

Babesia spp. (110, 118, 129)

BRUCE et al. (1915) published a painting of a piroplasm of an "edible rat". Many African rats are eaten, but perhaps none more enjoyed than *Thryonomys*. BRUCE's unnamed parasite (85) from Malawi was probably from this rodent.

Discussion

The habits and habitats of rodents are remarkably diverse. As SIMPSON (1959) wrote: "The total range of adaptations in the order is extraordinary and is probably not equaled by any other one order of organisms. Some are amphibious or nearly aquatic (e.g. the coypu) and some (e.g. Kangaroo mice) may never even touch water in their whole lives. Some are among the smallest of all mammals, some as

large as bears . . . Some plow like moles, some crawl, some hop on hind legs only, some gallop, some swim as well as ducks, many climb trees, some glide on wing-like membranes. They live from the polar regions to the equator and from the highest mountains to below sea level." The striking exploitation of ecological niches accompanied by such widely varying habits brings rodents into contact with many different blood-sucking arthropods. This provides an array of alternate vertebrate and invertebrate hosts required by the vector-borne blood-sporozoa which, in turn, appear to have well exploited the niches provided.

With such diversity, it is difficult to draw many firm conclusions about the true hostal and geographical distribution of the parasites dealt with in the present work. This is made even more difficult because the separate identities of very few of the parasites have been established by experiments in the laboratory, and many rodents have never been properly examined or, indeed, examined at all. Some patterns of distribution nevertheless emerge and a brief review, although certain to be inadequate, points the way to new work.

Hepatozoon is the commonest blood sporozoon of sciuriforms and myomorphs, with many records from rodents indigenous to Europe, Africa and Asia, and a few to America. Gametocytes of haemogregarines of all squirrels and most myomorphs are in leucocytes. The exceptions are the species parasitic in jerboas and gerbils, and in *Cricetomys*, *Dendromus* and *Otomys* which inhabit erythrocytes.

The wide distribution of haemogregarines of rodents is presumably due, at least in part, to the habits of the vectors (fleas, lice and mites) which permit sporogony to proceed largely unaffected by extremes of ambient temperature. Although transmission of several species has been achieved in the laboratory, in most instances the vector is unknown. The invertebrate host of *H. muris* of *Rattus* is the mite *Echinolaelaps echidninus* (= *Haemogamasus reidi*) in which all stages of sporogony have been seen (MILLER, 1908; SPLENDORE, 1918; KUSAMA et al., 1919; BRUMPT, 1946; KRAMPITZ, 1964). The sporogony of *H. griseisciuri* of the grey squirrel has been described in the same mite and in *Euhaemogamasus ambulans* (CLARK, 1958; REDINGTON & JACHOWSKI, 1971). *H. sciuri* of the red squirrel, however, is probably transmitted by the flea *Orchopeas wickhami* (DASGUPTA & MEEDENIYA, 1958). Several species of fleas have been shown to be the vectors of haemogregarines of microtine rodents (SPLENDORE, 1918; KRAMPITZ, 1964), but SPLENDORE (1918, 1920) found that the sporogonic stages of one such parasite, *H. pitymysi* of *Pitymys savii*, also developed in the louse *Haplo-neura acanthopus*. CHRISTOPHERS (1905) had earlier described the sporogony of *H. gerbilli*, an intra-erythrocytic parasite of the Indian gerbil, *Tatera indica*, in the louse *Haematospinosus stephensi*. Another intra-erythrocytic haemogregarine, *H. balfouri* of jerboas (*Jaculus* spp.),

develops in the mite *Haemolaelaps aegypticus* (HOOGSTRAAL, 1961; FURMAN, 1966). BALFOUR (1905), however, reported sporogonic stages of this parasite in the flea *Pulex cleopatrae*.

Piroplasms of rodents are less evenly distributed both hostally and geographically than the haemogregarines. There are numerous records of *Babesia* in myomorphs, especially gerbils, but comparatively few from sciuriforms. In the Far East and S. America there are only few reports of *Babesia* in rodents other than *Rattus*. DUNN et al. (1968) looked at the blood of many W. Malaysian rodents but recorded no piroplasms, and LAINSON (personal communication) has examined several thousand Brazilian rodents without encountering *Babesia*. This apparent rarity of piroplasms of rodents in some places is important when considering the source of infection of rare cases of piroplasmosis of man such as those recorded from Yugoslavia (SKRABALO & DEANOVIC, 1957), the U.S.A. (SCHOLTENS et al., 1969; BENSON et al., 1969), and the Republic of Eire (FITZPATRICK et al., 1968).

Little is known of the transmission of piroplasms of rodents. KRYLOV (1964) studied the development of *B. tadjikistanica* in the tick *Hyalomma anatolicum* and found that although the parasite multiplied in larvae, the salivary glands did not become infected until after the larval moult. Forms infective to gerbils did not develop until after the nymph had taken a bloodmeal. Transovarial transmission of the piroplasm in the tick did not occur. FAY & RAUSCH (1969) noted that splenomegaly of voles in Alaska co-occurred with the distribution of *Ixodes angustus*. This led to a successful transmission in the laboratory of an unnamed piroplasm of the vole *M. oeconomus* by the bite of nymphs of this tick which had been experimentally infected as larvae. Progeny of a naturally infected tick failed to infect laboratory-bred voles. In England, YOUNG (1970) transmitted *B. microti* to laboratory rats and mice by the bite of nymphs of *Ixodes trianguliceps* experimentally infected as larvae.

Hepatocystis is unknown in any host in the New World or Australasia, and it appears to be restricted to the Old World Tropics where it has been recorded from monkeys, the mouse-deer, the hippopotamus, bats and squirrels. The species infecting squirrels are from Asia, and although *Hepatocystis* is common in monkeys in Africa (see GARNHAM, 1966), it has never been recorded in an African rodent. Sporogony of none of the species infecting rodents has been seen, and the vectors are unknown. Presumably they are midges (*Culicoides* spp.), the proven vectors of *H. kochi* of African monkeys (GARNHAM et al., 1961).

As with *Hepatocystis*, *Plasmodium* is not known in New World rodents. Malaria parasites of mammals other than man are poorly represented in that continent; two species, *P. simium* and *P. brasilianum*, are known from S. American monkeys, and an unnamed malaria para-

site has been reported in deer from Texas (KUTTLER *et al.*, 1967). Murid rodents, among which are hosts of *Plasmodium* in Africa, are not indigenous to the New World, and it is tempting to assume that true malaria parasites are absent in South American rodents of other families.

Species of *Plasmodium* of rodents are known from (i) semi-arboreal African murines of the Lower Guinea Forest, (ii) two African and five Asian flying squirrels and (iii) the African brush-tailed porcupine. With the exception of the last of these animals, infections of which are acquired in a restricted biotope in caves (MOUCHET *et al.*, 1957), wholly terrestrial rodents seem not to occupy a niche where they are likely to become part of an anopheline-malaria-rodent complex. In the vast Neotropical forests, arboreal rodents would appear to be the ones most likely to harbour malaria parasites.

The vectors of malaria parasites of flying squirrels of Asia and Africa are unknown. These hosts are phylogenetically distant but their similar habits presumably bring them into close contact with mosquitoes living in tree-holes or the forest canopy. Evidence is slowly accumulating that there is a high prevalence of malaria in these animals, and in suitable localities it should not be difficult to find the vectors. The possibility that transmission may be seasonal and perhaps limited to a very short period must be borne in mind.

P. atheruri of the brush-tailed porcupine of Africa is transmitted in nature by the largely cavernicolous anopheline *A. smithii* (MOUCHET *et al.*, 1957; VAN DEN BERGHE *et al.*, 1958) and perhaps by other mosquitoes of the *smithii* section, series *Neomyzomyia*, subgenus *Cellia* (GILLES & DE MEILLON, 1968). Sporozoites in the salivary glands of wild-caught *A. smithii* cannot, however, be assumed always to be *P. atheruri* since in at least one part of Africa (Ghana) *A. smithii* transmits a malaria parasite of fruit bats (VAN DER KAAJ, 1964; BRADY, 1965).

P. atheruri has not been transmitted cyclically in the laboratory. Using the mouse adapted strain of LANDAU *et al.* (1969a) I have obtained the sporogonic stages in laboratory-bred mosquitoes, but sporozoites were never infective to splenectomized mice (unpublished). The development of the parasite at different temperatures in eight species of *Anopheles* was as follows: (i) ookinetes formed, but no oocysts were seen: – *A. albimanus* (21 °C), *A. melas* (24 °C), *A. sudaicus* (24 °C), *A. farauti* (28 °C) and *A. freeborni* (28 °C); (ii) oocysts grew to maturity, but salivary glands not invaded by sporozoites: – *A. gambiae* (20 °C) and *A. stephensi* (24 °C, 28 °C); (iii) oocysts grew to maturity and salivary glands invaded, but sporozoites not infective: – *A. labranthiae atroparvus* (22 °C) and *A. freeborni* (22 °C). The better development in *A. freeborni* at 22 ° compared to 28 °C suggests that the most

suitable temperature for the healthy sporogony of *P. atheruri* is probably low.

In Africa, the distribution of the malaria parasites of murine rodents is apparently restricted to the periphery of the Lower Guinea or Congo Forest, which extends from Katanga in the east, to Nigeria in the west. In Katanga, *Anopheles durenii millecampsii* is the natural vector of *P. berghei* and *P. v. vinckei*. In lowland localities in other parts of Africa (Central African Republic, Brazzaville and Nigeria) where this mosquito is absent, the invertebrate hosts of *P. yoelii* and *P. vinckei* spp. are unknown. There is, however, some evidence that *A. cinctus* may be implicated. In the laboratory, *P. berghei* and *P. yoelii* have been successfully transmitted with experimentally infected *A. stephensi*, *A. labranchiae atroparvus*, *A. annulipes*, *A. gambiae* A, B, *A. aztecus*, *A. quadrimaculatus* and *A. sundaicus*. Subspecies of *P. vinckei*, however, have been transmitted cyclically in the laboratory only with *A. stephensi*; a number of other laboratory-bred anophelines have been found to be unsuitable hosts (see the review by KILLICK-KENDRICK, 1971).

The principal vertebrate hosts of the murine parasites are *Thamnomys* and *Grammomys*, semi-arboreal rodents which flourish in secondary forest formed by the farming activities of man, or in forest galleries. A number of negative surveys have been carried out in the Upper Guinea Forest west of the Dahomey Gap (KILLICK-KENDRICK, 1971). In this part of Africa, arboreal murids appear to be scarce or difficult to catch, and although *Thamnomys* and *Grammomys* occur, they are seldom encountered. Bellier (*personal communication*) suggests they have been largely replaced by another semi-arboreal rodent, the little-known *Dephomys*, following harsh competition among silvatic rodents during desiccation and fragmentation of the Upper Guinea block some time well into the late Pleistocene (MOREAU, 1963, 1964). The vicissitudes of this part of the African forest must also have affected the silvatic anophelines, and possibly malaria parasites are not present in murids in this most westerly part of the continent.

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Zusammenfassung

Die Arbeit gibt eine Zusammenstellung der blutparasitierenden Protozoen in Nagetieren. Soweit sie bekannt sind, werden die Wirte aufgeführt und die geographischen Gebiete genannt, in welchen die Parasiten auftreten. Haemogregarinen der Gattung *Hepatozoon* wurden bisher bei 67 Nagetierarten gefunden; sie stellen die häufigsten und am weitesten verbreiteten Blutsporozoen der Sciuromorpha und Myomorpha dar. Die Mehrzahl der Fundberichte stammt aus der paläarktischen, der äthiopischen und orientalischen Region. Die Gametocyten finden sich in Leukocyten, außer bei jenen Arten, welche Springmäuse, Wüstenmäuse, *Cricetomys*, *Dendromys* und *Otomys* parasitieren, wo Erythrocyten befallen werden. Da – mit wenigen Ausnahmen – die Gametocyten morphologisch voneinander nicht zu unterscheiden, und da nur wenige Lebenszyklen bekannt sind, ist die Zahl der Arten, die in Nagetieren parasitieren, nicht wirklich bekannt.

Piroplasmen der Gattung *Babesia* stellen die nächst häufigsten Blutsporozoen von Nagetieren dar; sie wurden bisher in 57 Arten beschrieben. Piroplasmen

sind bei Nagetieren der neoarktischen, palaearktischen und äthiopischen Region besonders häufig, hingegen bei Nagern der neotropischen, orientalischen und australasiatischen Region selten. Mit Ausnahme der Murmeltiere zählen nur wenige Sciuromorpha zu den Wirten; am häufigsten werden Babesien bei Myomorpha, insbesondere bei Wüstenmäusen gefunden. Die Artzugehörigkeit zahlreicher Piroplasmen ist zweifelhaft.

Für *Hepatocystis* sind unter den Nagetieren einzig Eichhörnchen der orientalischen Region als Wirte bekannt; 16 Arten wurden als solche bezeichnet. *Rayella*, eine verwandte haemoproteide Gattung, wurde bei 4 indischen Flughörnchenarten beschrieben.

Echte Malariaparasiten (*Plasmodium*), sind von 5 afrikanischen Muriden, 2 afrikanischen Anomaluriden, von der Gattung *Atherurus* sowie von 5 asiatischen Flughörnchenarten bekannt; von Nagetieren der neotropischen Region sind keine Plasmodien beschrieben worden.

Résumé

Une liste des Protozoaires parasites de cellules sanguines des Rongeurs a été établie. On y trouve également les hôtes connus et les régions où les parasites ont été trouvés. Les Hémogregarines du genre *Hepatozoon* ont été trouvées chez 67 espèces de Rongeurs; il s'agit des Sporozoaires les plus fréquents et les plus répandus parmi les Sciuromorphes et les Myomorphes. La plupart des références concerne les régions paléarctique, éthiopienne et orientale. Les gamétocytes des parasites vivent dans les leucocytes, à l'exception des espèces qui parasitent les Gerboises, les Gerbilles, *Cricetomys*, *Dendromus* et *Otomys*; chez ces espèces, les gamétocytes vivent dans les hématies. Les gamétocytes des différentes espèces ne peuvent être distingués par leur morphologie, à quelques exceptions près; d'autre part, seuls quelques cycles biologiques ont pu être établis, si bien que le nombre véritable des espèces parasitant les Rongeurs n'est pas connu.

Les Piroplasmes du genre *Babesia* sont, après *Hepatozoon*, les Sporozoaires les plus fréquents dans le sang des Rongeurs: on les a trouvés chez 57 espèces. Ces parasites sont particulièrement communs chez les Rongeurs des régions néarctique, paléarctique et éthiopienne; par contre, ils ne sont pas communs chez les Rongeurs des régions néotropicale, orientale et indo-australienne. Les Sciuromorphes autres que les Marmottes servent rarement d'hôtes; la plupart des références concernent des Myomorphes, en particulier les Gerbilles. L'identification de l'espèce de beaucoup de Piroplasmes est douteuse.

Parmi les Rongeurs, *Hepatocystis* n'a été trouvé que chez les Ecureuils de la région orientale: 16 espèces y sont connues en tant qu'hôtes. Un Hémoprotéide apparenté, *Rayella*, a été trouvé chez 4 Ecureuils volants des Indes.

Les véritables parasites du Paludisme (*Plasmodium*) sont connus chez 5 espèces de Murinés africains, 2 espèces d'Anomaluriné, le Porc-épic africain et 5 espèces d'Ecureuils volants d'Asie. On ne les a pas trouvés chez des Rongeurs de la région néotropicale.