

DISTRIBUTION OF WILD-RODENT PLAGUE

P. C. C. GARNHAM, M.D., D.P.H.

*Reader in Medical Parasitology,
London School of Hygiene and Tropical Medicine*

Member of the Expert Committee on Plague of the World Health Organization

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Plague may be regarded as falling into the following four categories—epidemic, endemic, epizootic and enzootic. It can also be classified as human plague, and domestic- and wild-rodent plague. The last form was called sylvatic or selvatic plague by Jorge in 1928 ; but Pozzo and Girard have pointed out that the term is a misnomer, as wild-rodent plague is essentially of the steppe, veldt or plain, and not of the forest. The term “wild-rodent” itself is not sufficiently comprehensive, as the disease affects also shrews, opossums, and even carnivora.

Plague in man and the domestic rat is fairly well understood and the world situation regarding it is fairly exactly defined. Methods for its control exist, and its spread in these forms can be fairly easily checked, particularly since the advent of DDT. But plague in the wild rodent is another matter. Its geographical limits are known precisely in only a few countries ; many of the carrier species and their fleas still remain undiscovered ; the relation of wild-rodent plague to human outbreaks is not properly understood ; and, above all, a satisfactory method for its eradication has yet to be found.

The dividing line between wild-rodent plague and plague affecting domestic rodents has to be drawn arbitrarily, because certain field-rats are also, to a lesser extent, house-rats, while some rodents which were originally domestic have now been driven into the field by the black rat, e.g., as has happened in the case of the multimammate mouse in parts of Africa. For the purpose of this summary, it is convenient to exclude *Rattus rattus* and *Rattus norvegicus*, but to include rodents such as *Arvicanthis abyssinicus* and *Mastomys coucha*, because they spend much of their lives in rural surroundings. The criteria of sylvatic plague drawn up by Macchiavello (1941) are probably the best ; they are as follows :

- (1) it occurs independently of domestic-rat infection ;
- (2) it appears among wild rodents with *Pasteurella pestis* demonstrable either in the rodents or in their fleas ;
- (3) there is an absence of fleas other than those of the wild rodents.

The foci of wild-rodent plague may be divided into two fundamentally distinct groups. The first group includes the foci where wild rodents are

primarily involved in the infection. This is the type of focus found in Central Asia. The second group includes foci in which wild rodents are secondarily involved in infection with plague. Such animals become infected through contact with diseased rats of ports, etc., often through the medium of a 'liaison carrier'. Thus in South Africa, infection passes from the domestic *Rattus rattus rattus* to the domestic striped mouse *Rhabdomys pumilio* and thence to the gerbils of the veldt. Foci of this second type have been clearly defined in California, South Africa, and South America.

Until now, the secondary form of wild-rodent plague seems to have been accompanied by no large-scale human epidemics. In the USA, where the fields may be littered with the bodies of rodents dead of plague, human cases are rare; in fact, up to 1948 only 66 cases of plague have been traced to sylvatic outbreaks in that country.

The following survey does not include records of wild-rodent plague of ancient date, such as the infection in hares which has long since disappeared from England. There is clear proof of the present existence of this form of the disease in North and South America, Central Asia and South Africa, but elsewhere in Africa, in the East Indies, India, Madagascar, and the Pacific Isles, its existence is doubtful. The ecology of wild-rodent plague is most complex; to unravel it is like following the different voices in a Bach fugue, except that in plague the basic design is unknown.

The animals named in these lists have all been found spontaneously infected with plague, or are strongly suspect on epidemiological grounds. These lists are not complete, but include the more important reservoir hosts.

USSR, including Outer Mongolia

Foci here are of the primary type and have given rise to large-scale epidemics, but most of these foci now appear to be quiescent, except those in south-eastern Russia. The Siberian and Mongolian epidemics are associated with infected marmots (tarabagans) and a species of *Cynomys* (susliks). Plague persists in these animals during their long hibernating period. In south-eastern Russia, the principal reservoir is *Citellus pygmaeus*, with jerboas, voles and gerbils playing usually minor roles. In the sandy regions of Transcaspia, the merion is the chief rodent carrier, with mice acting in a liaison capacity.

Transbaikalia (also parts of northern China)

<i>Marmota bobak</i>	<i>Lasiopodomys brandti</i> and other
<i>Citellus dauricus</i>	species of voles
<i>Allactaga mongolica</i>	

Southern Kirghisia

Marmota caudata

South-eastern Russia

<i>Citellus pygmaeus</i>	<i>Ellobius talpinus</i>
<i>Cynomys fulvus</i>	<i>Cricetus cricetus</i>
<i>Meriones tamaricinus</i>	<i>Allactaga saliens</i> and other
<i>Microtus arvalis</i>	jerboas
<i>Lagurus lagurus</i>	<i>Dipus sagitta</i>

Transcaspia and Turkestan

<i>Meriones meridianus</i>	<i>Lepus europaeus</i>
<i>Rhombomys opimus</i>	

Asia

Wild-rodent plague does not occur to any extent in India and Ceylon. Most of the following rodents become infected from time to time through contact with domestic rats.

Ceylon

<i>Funambulus palmarum</i>	<i>Bandicota gracilis</i>
<i>Bandicota malabarica</i>	

Southern India

<i>Funambulus</i> sp.	<i>Bandicota malabarica</i>
<i>Mus booduga</i>	<i>Bandicota kok</i>
<i>Golunda ellioti</i>	<i>Tatera</i> sp.

Northern India

<i>Bandicota indica</i>
<i>Bandicota bengalensis</i>

East Indies

Records from the plague areas of the East Indies do not appear to demonstrate the clear existence of sylvatic plague, though the infection has been reported in field rats and in two species of shrews (*Crocidura murina* and *C. caerulea*).

Africa**South Africa**

Plague has spread from the urban rats of the ports to the gerbils, karoo-rats, and other rodents of the interior and has caused nearly a thousand outbreaks of the disease in rural areas. Wild-rodent plague is now widespread and is still active ; all parts of the Union are affected except for certain areas in the Cape, the Natal mountains and the Transvaal. The

infection has spread in a westerly direction through the Kalahari Desert to South-West Africa and Bechuanaland, and through the Orange Free State into Angola, Basutoland and the Rhodesias.

<i>Tatera lobengulae</i> and other gerbils	<i>Desmodillus auricularis</i>
<i>Geosciurus capensis</i>	<i>Myotomys granti</i> and other veldt rats
<i>Mastomys coucha</i>	<i>Malacothrix typicus</i>
<i>Rhabdomys pumilio</i> and other field-mice	<i>Lepus capensis</i> and other hares

South-West Africa

Mastomys coucha
Tatera schinzi

Angola

Sylvatic plague spread to Angola from Ovamboland through the medium of gerbils, hares, etc.

Mastomys coucha
Microtus sp.

Mozambique

Cricetomys gambianus

Bechuanaland and the Rhodesias

Severe outbreaks of sylvatic origin have occurred involving over 300 human beings, but the epizootics have declined since 1945. In addition to the list below, about 25 other rodents of less importance have been incriminated.

<i>Tatera brantsi</i> and other gerbils	<i>Pedetes cafer</i>
<i>Mastomys coucha</i>	<i>Lepus</i> sp.
<i>Thallomys damarensis</i> and other tree-rats	<i>Geosciurus inauris</i>

Nyasaland

Mild outbreaks of sylvatic origin have been reported in recent years.
Saccostomus campestris

Senegal

Plague appears to be confined to the Senegal littoral ; it is absent in the interior and in other French West African territories. The domestic rat plays the principal role in plague transmission on the west coast and the existence of true sylvatic plague is doubtful.

<i>Crocidura stampflii</i>	<i>Cricetomys gambianus</i>
<i>Xerus erythropus</i>	<i>Pelomys campanae</i>

<i>Mastomys coucha</i>	<i>Lepus</i> sp.
<i>Arvicanthis rufinus</i>	

Gold Coast

Cricetomys gambianus

Belgian Congo

Active foci of sylvatic plague exist near Lake Albert ; in 1939 there were 65 human cases, which were ascribed to this source. Infected rodents are present in the provinces of Stanleyville and Costermansville.

<i>Mastomys coucha</i>	<i>Otomys tropicalis</i>
<i>Leggada</i> sp.	<i>Lemniscomys striatus</i>
<i>Arvicanthis abyssinicus</i>	<i>Pelomys</i> sp.
<i>Lophuromys aquilus</i>	<i>Dasymys bentleyae</i>

East Africa (Kenya, Uganda and Tanganyika Territory)

Although epizootics of a fatal disease among field-rodents have often been observed, there appears to be no proof that any of these were really due to *P. pestis*, and most of the human plague is of domestic origin. The following rodents are suspect on epidemiological grounds :

<i>Mastomys coucha</i>	<i>Otomys</i> sp.
<i>Pelomys fallax</i>	<i>Arvicanthis abyssinicus</i>
<i>Grammomys</i> sp.	<i>Lemniscomys massaicus</i>

Egypt

The part played by field-rats in plague in Egypt has not been fully assessed. The following two rodents are probably of some importance, but surveys in the Suez Canal Zone indicate the presence of suitable rodents (e.g. gerbils).

Arvicanthis niloticus
Acomys cahirinus

North Africa

The existence of sylvatic plague in North Africa has not been definitely established, though suitable rodents exist, such as *Xerus getulus* and *Psammomys roudairei* in the southern parts, and *Gerbillus hertipes* in Tripolitania. Fortunately plague is largely absent from these regions, and, where it is endemic, there appear to be no very susceptible wild rodents.

Madagascar

There is some doubt whether true sylvatic plague exists on this island.

Brachytarsomys albicauda

North America

Plague spread early in the century from the domestic rats of San Francisco to the ground-squirrels of California, and the infection has now extended to many States, including Alberta in Canada. This secondary focus remains active and involves many types of animals, particularly squirrels, chipmunks and prairie-dogs, while wood-rats, field-mice, hares and other small rodents act as complementary hosts and help to spread the disease. Human cases have been most numerous in California, with a few in Nevada, Oregon, Utah, Idaho and Alberta ; the plague which has occurred in Louisiana, Texas and Florida may not be of sylvatic origin.

California

<i>Citellus leucurus leucurus</i>	<i>Marmota flaviventris</i>
<i>C. beldingi parvulus</i>	<i>Tamias frater</i>
<i>C. beldingi oregonus</i>	<i>Glaucmys sabrinus lascivus</i>
<i>C. beldingi beldingi</i>	<i>Cynomys parvidens</i>
<i>C. townsendi mollis</i>	<i>Thomomys bottae</i>
<i>C. lateralis chrysodeirus</i>	<i>Neotoma</i> (several species of wood-rats)
<i>C. lateralis lateralis</i>	
<i>C. beecheyi beecheyi</i>	<i>Peromyscus truei truei</i>
<i>C. beecheyi douglasii</i>	<i>Reithrodontomys megalotis</i>
<i>C. beecheyi nudipes</i>	<i>Microtus californicus</i>
<i>C. beecheyi fisheri</i>	<i>Lepus bairdi</i>
<i>Tamiasciurus douglasii albolimbatus</i>	<i>Sylvilagus bachmani</i> ^a

Nevada

<i>Citellus beldingi oregonus</i>	<i>Citellus armatus</i>
and other species of ground-squirrels	<i>Neotoma cinerea occidentalis</i>

Oregon

<i>Citellus beldingi oregonus</i>	<i>Marmota flaviventris avara</i>
and other species	<i>Taxidea taxus neglecta</i>

Utah

<i>Citellus variegatus grammurus</i>	<i>Neotoma cinerea occidentalis</i>
<i>Marmota flaviventris engelhardti</i>	

Idaho, Montana, Wyoming

<i>Citellus richardsoni richardsoni</i>	<i>Cynomys ludovicianus ludovicianus</i>
and other species	<i>Marmota flaviventris</i>

^a This rabbit is also a carrier of tularaemia.

North Dakota

Citellus richardsoni richardsoni
and other species

New Mexico

<i>Citellus tridecemlineatus</i>	<i>Neotoma albigula albigula</i>
and other species	<i>Onychomys</i> sp.
<i>Cynomys leucurus zuniensis</i>	<i>Dipodomys ordii ordii</i>

Colorado

<i>Citellus variegatus grammurus</i>	<i>Marmota flaviventris</i>
<i>Cynomys leucurus zuniensis</i>	

Oklahoma

Neotoma sp.

Kansas

Cynomys sp.

Washington

<i>Citellus washingtoni loringi</i> and other ground-squirrels	<i>Sylvilagus nuttallii nuttallii</i>
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Alberta, Canada

Citellus columbianus

Saskatchewan, Canada

Citellus richardsoni

South America

Wild-rodent plague in South America is peculiar in that it affects chiefly the guinea-pigs and the cricetids, sometimes in the form of a chronic or sub-acute disease.

Argentina

Appalling epizootics among the field rodents have occurred during the last decade and the infection has spread throughout the country from the north to Patagonia. There have been many human cases of sylvatic origin. It is stated that at least 70 species of wild rodents, in addition to those listed below, have shown the infection.

<i>Galea musteloides</i>	<i>Lepus</i> sp.
<i>Caviella australis australis</i>	<i>Ctenomys</i> sp.
and other guinea-pigs	<i>Sylvilagus brasiliensis</i>
<i>Graomys griseoflavus</i>	<i>Hesperomys muriculus</i>
<i>Lagostomus</i> sp.	

Brazil

Plague is still a dangerous menace. Macchiavello (1941) suggests that the opossum *Monodelphis domestica* acts as the liaison between domestic and wild animals.

<i>Oryzomys sylvaticus</i>	<i>Lepus</i> sp.
<i>Reithrodontomys minusculus</i>	<i>Cavia aperea</i>
<i>Oryctolagus cuniculus</i>	

Ecuador

Cavia aperea

Venezuela

The disease is mild and has not occurred since 1943.
Sigmodon hirsutus

Bolivia

The disease has been imported from Argentina.
Sylvilagus brasiliensis
Cavia sp.

Peru

Wild-rodent plague occurs near the Ecuador border.

<i>Sciurus stramineus</i>	<i>Rhipidomys equatoris</i>
<i>Oryzomys xantheolus</i>	<i>Akodon mollis</i>
<i>Oligooryzomys longicaudatus</i>	<i>Cavia aperea</i>

PRINCIPAL WORKS CONSULTED

- Chabaud, A. G. (1947) *Ann. Parasit. hum. comp.* **22**, 169, 357
 Davis, D. H. S. (1948) *Ann. trop. Med. Parasit.* **42**, 207
 Ellerman, J. R. (1940-1941) *The families and genera of living rodents*, 2 vols., London
 Hubbard, C. A. (1947) *Fleas of western North America*, Ames, Iowa
 Macchiavello, A. (1941) *Contribuciones al estudio de la peste bubónica en el nordeste del Brasil*, Washington, D.C. (Oficina Sanitaria Panamericana, Publ. No. 165)
 Meyer, K. F. (1942) *Amer. J. trop. Med.* **22**, 9
 Pozzo, A. A. (1945) *Peste de oriente*, Buenos Aires
 Wu Lien-Teh (1936) *Plague*, Shanghai
- Bulletin mensuel de l'Office International d'Hygiène Publique*
Public Health Reports, Washington
Tropical Diseases Bulletin