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RODENT RESERVOIRS & FLEA VECTORS OF NATURAL FOCI OF PLAGUE

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Rodent reservoirs

Plague is primarily a disease of rodents. The infection is maintained in natural foci of the disease in wild rodent colonies through transmission between rodents by their flea ectoparasites. For the most part, the sylvatic rodent reservoirs are species that are susceptible to the infection but resistant to the disease. While upwards of 200 species of rodents and lagomorphs have been implicated in the epidemiological cycle of plague in one geographical area or another, the true number of rodent species important as more than accidental reservoirs of plague is uncertain.

Many species of rodents and other small mammals are susceptible to infection but are only occasionally infected and are not necessarily important reservoirs of infection. The animal hosts of plague are classified as enzootic (maintenance) hosts and epizootic (amplification) hosts (1). The first group includes rodents from genera that are relatively resistant to plague. In this group mortality from plague infection is low, although antibody surveys of field populations may show a positivity rate as high as 100%. Die-offs commonly seen among more susceptible rodent species are rare in this group. The plague organism is occasionally introduced into colonies or areas of more susceptible species. This occurs in nature by an overlap of individuals or populations of two species. When this happens in a species that is highly susceptible to plague, an epizootic – sometimes of considerable magnitude – may occur, and high mortality (rodents positive for plague) is seen in sylvatic and peridomestic areas or even in villages or cities.

It is difficult to group the many different species of rodents, lagomorphs and other small mammals involved as common or occasional reservoirs or hosts of plague to fit the above classification. The susceptibility to plague infection of a given species may vary even within

the geographical limits of a foci. Furthermore, susceptibility may vary temporally with variations in the density of the host populations or in the density of their flea ectoparasite vectors. The virulence of the particular strain of the plague bacterium involved in the epizootic may also vary over a period of time.

As most of the natural foci of plague have existed for long periods of time, it is clear that a portion of any reservoir population must survive infection. In some species the infection can continue to circulate with relatively little mortality (2).

Flea vectors

About a dozen cosmopolitan species are implicated in the transmission of domiciliary plague (3). However, many more species of the order *Siphonaptera* have been implicated in the transmission of sylvatic plague (4).

To understand the epidemiology and transmission of the infection from rodent reservoirs to human hosts, it is essential to determine the flea species involved in plague transmission in a given area. Information on the bionomics of the flea vectors is basic to their control and control of transmission of the infective agent. The following section provides information on the most important flea vectors of plague in the various endemic foci. If this information is not already available for an area in which plague is suspected or known to be endemic, surveys of flea ectoparasites should be done. Survey methods are described elsewhere in this publication.

Entomological expertise is needed for the design, implementation and (particularly) identification of the flea species taken and evaluation of their importance in relation to plague transmission.

Cosmopolitan vectors of plague

The majority of the flea species described below are ectoparasites of commensal or peridomestic rodents. Because of their close proximity to humans and their dwellings, these fleas are often found on livestock and household animals. Most of these species have a wide distribution, although their percentage in the flea population varies from place to place as does their role as vectors of plague. All, however, readily feed on humans. The commensal rodent fleas are classed as follows (5):

- (1) Fleas specific to commensal rodents which show a wide distribution and are found in several plague-endemic areas. *Xenopsylla cheopis* (Oriental rat flea) has a wide distribution, while the distribution of *X. brasiliensis* and *Nosopsylla fasciatus* is more limited.
- (2) Species specific to commensal rodents which show a limited or even restricted geographical distribution, such as *X. astia*.
- (3) Wild rodent fleas which frequently infest commensal rodent species.
- (4) Flea species which, because they are common in the environment of commensal rodents, are often found in limited numbers on these rodents although they are not specific for them. *Echidnophaga gallinacea* and *Pulex irritans*, both of which have a cosmopolitan distribution, and the cat flea, *Ctenocephalides felis*, are examples of this latter group.

To act as an efficient plague vector, the flea must be able to ingest the plague organism with its blood meal. Second, it must live long enough for the pathogen to multiply sufficiently. Third, it must be able to transfer the pathogen to an animal or human host in sufficient concentrations to cause an infection and last, it must be present in large enough numbers to maintain the infection in the local rodent hosts (6). There are a number of other characteristics but these are the most important.

When a flea sucks blood from an infected rodent or other host, some of the bacteria settle on the flea's proventriculus. This spined structure shuts off the stomach while the flea is sucking but opens to allow ingested blood to enter the stomach. Plague bacteria that have settled on the spines of the proventriculus multiply and eventually block the passage of blood into the stomach. Although the flea continues to feed (with increasing avidity as time passes) blood cannot continue to enter its stomach and instead remains in the oesophagus. When the flea stops sucking, the oesophagus recoils and the accumulated blood is driven into the bite wound, bringing *Y. pestis* with it. A flea in this condition is known as a "blocked" flea. Those species of fleas most subject to blocking are the most efficient vectors of plague, providing that the other requirements of transmission are met and that the flea survives long enough to transmit the infection.

Xenopsylla cheopis is the most important vector of plague and the rickettsial infection murine typhus. The species is thought to have originated in Egypt but during the 19th century spread to all parts of the

world as parasites of rats infesting ships' cargos. A high incidence of plague-infected *X. cheopis* in a given focus, greatly increases the risk of transmission to humans. *X. cheopis* most commonly parasitizes *Rattus* species but is frequently found on other rodent species in and around houses.

Xenopsylla astia is a parasite of both gerbils and rats. It ranges from the Arabian peninsula through Iran to southeast Asia and to Korea (7) and has been found on the east coast of Africa. It is a less efficient vector than *X. cheopis*.

Xenopsylla brasiliensis is native to all Africa south of the Sahara where it is the most common vector in some areas (8), often more common than *X. cheopis*. It has spread to other parts of the world such as Brazil and India. It is an effective plague vector, especially in rural environments. It is less tolerant of high temperatures than *X. cheopis* but is more resistant to drought conditions.

Nosopsyllus fasciatus, the Northern rat flea, is one of the most prevalent fleas in Europe on commensal rats (9). Its distribution is virtually global and it is found from the United States to China (10) and Korea (11). Its numbers appear to be increasing in Japan (12). It is also found on mammals and rodents other than *Rattus* and feeds freely on humans. It is relatively unimportant as a vector of plague.

Monopsyllus anisus is the common rat flea of temperate east Asia, extending from China and Transbaikalia Russia to Japan. It has been found in ports in San Francisco and Vancouver and in the United Kingdom.

Leptopsylla segnis, the mouse flea, probably originated in western Asia on *Mus* or *Apodemus*. It is generally abundant on rats than on mice. It is widely distributed, particularly in temperate areas, but is only a weak vector of plague and an uncertain vector of murine typhus (13).

Pulex irritans, the human flea, was considered to have originated as an Old World species (3) but a more recent review (14) observes that the species probably originated in South or Central America as an ectoparasite of the guinea pig or peccary. *P. irritans* is now worldwide in its distribution. Despite its common name it has a wide range of hosts: it is found in the wild on foxes, badgers, ground squirrels, guinea pigs and rats as well as domestically on pigs, goats, dogs, cats and humans. It is often found in high densities in habitations. *P. irritans* has been considered as a

possible or probable vector of plague in Angola (15), Brazil (16), Burundi (17), the Democratic Republic of the Congo (21), Iran (2), Iraq (18), Nepal (19), and Tanzania (20).

Ctenocephalides felis, the cat flea, has become completely cosmopolitan in its distribution. It is frequently found not only on cats but also on a large number of other hosts, including dogs, humans, other mammals and birds (22). There appears to be a gradual northern extension of this species (12). It may be a vector of murine typhus and is also an intermediate host of some cestodes. Both the cat flea and the dog flea (*Ctenocephalides canis*) are able to transmit plague to humans from pet animals.

The following section considers the main rodent reservoirs and flea vectors of plague in most of the better-known endemic foci. Some foci are large and contiguous—such as those in the western United States, the Russian Federation, China and Mongolia—and extend across borders to more than one country. In foci such as these, reservoir and flea vector species may differ considerably from one part of the focus to another.

Plague reservoirs and vectors in Africa

Plague foci of southern Africa (23,24,25,26,27,28,29,30)

This area includes foci in South Africa, Lesotho, Namibia and Zimbabwe. Although the number of plague outbreaks in this sub-region have declined considerably in recent years, the infection persists in many areas where human plague has not been apparent for years. It is therefore important to understand the mechanism and the rodent species responsible for persistence in the natural foci.

The main reservoir in many parts of this geographical region was long thought to be the gerbil, *Tatera brantsi*. The passage of plague infection in Orange Free State, South Africa, has been traced from gerbils as the reservoir to other wild rodents, *Otomys irroatus* to *Mastomys natalensis* to *Rattus rattus* and to humans. *M. natalensis* is now understood to be a species complex: early studies have separated it into species A and B. The distribution of human plague in southern Africa is apparently linked to the distribution of species B of the *Mastomys*(*Praomys*) *natalensis* species complex.

Studies have been done to determine if the sibling species of *M. natalensis*, *Aethomys chrysophilus*, *Mastomys coucha*, *Tatera leucogaster* and

A. namaquensis differed in their potential as reservoirs of plague in southern Africa. *M. natalensis* with 32 diploid chromosomes was significantly more resistant to experimental plague infections with high level inoculations of *Y. pestis* than *M. coucha* with 36 diploid chromosomes. The geographic distribution of human plague in southern Africa corresponds closely with that of the plague-susceptible species, *M. coucha*, while the plague-resistant species *M. natalensis* predominates in areas where human plague has not been recorded. *A. namaquensis* is extremely plague-sensitive, much more so than *A. chrysophilus*, and they may play different roles in the plague cycle.

In an outbreak of plague in Coega in the Cape Province of South Africa in 1982 plague antibody was found in two rodent species: the four-striped mouse, *Rhabdomys pumilo* and the vlei rat, *Otomys irroratus*. Sera from 3012 rodents of 24 species captured in South Africa were tested for antibody to the Fraction 1 antigen of *Y. pestis* by passive haemagglutination. Of 24 species investigated, antibodies were found in seven (0.23%) rodents of three species, *Desmodillus auricularis* and *Tatera brantsii* in the northern Cape Province and in *R. pumilo* in the eastern Cape Province.

The gerbils *Tatera brantsi*, *T. leucogaster* and *T. afra* play an important role in southern African plague epidemiology. *Rhabdomys pumilio* and *Otomys irroratus* were found infected in Cape Province in studies carried out in 1982 (29) .

The fleas most frequently found on the rodent reservoirs of plague are *X. philoxera*, *X. brasiliensis* and *Dinopsyllus ellobius*. However, in ports and coastal towns *X. cheopis* is the dominant flea species on *Rattus* species and is the dominant flea vector of plague.

In Zimbabwe, *T. leucogaster* and *M. coucha* are highly susceptible to plague and die soon after infection, making it unlikely that they act as reservoir hosts. Because they are relatively resistant to plague, *Aethomys chrysophilus* and *M. natalensis* are the more likely reservoirs. In Zimbabwe both *M. coucha* and *M. natalensis* are semi-domestic and probably act as a link between humans and the true sylvatic foci of plague (30).

Plague foci of East Africa

This area includes plague-endemic regions of Kenya, Tanzania, Mozambique and Madagascar. Plague is widely endemic in the four countries.

Kenya (31,32,33,34)

In an early survey of rodents for plague in a plague focus near Rongai, north of Nakuru, plague was isolated from five species of wild rodents: *Otomys angoniensis*, *Arvicanthis abyssinicus*, *M. natalensis*, *Lemniscomys striatus* and *Rhabdomys pumilo*. The reservoirs of plague have been extensively studied in Kenya. Sera from 8,860 rodents and other small mammals were examined for antibodies to *Y. pestis* in one survey, where it was noted that enzootic plague in Kenya is much more widely distributed than the human cases reported. *A. niloticus*, *M. natalensis* and *R. rattus* are probably the most important and widespread reservoirs of plague in Kenya. Ten percent of all *R. rattus* tested were found to be positive, as compared to 12% of the *Arvicanthis*. *Tatera robustis* has also been found positive at a low level. The high prevalence of plague antibodies in *R. rattus* is significant, in that the species readily lives both as a commensal and wild species and thus can serve to introduce plague from its sylvatic reservoirs into a commensal cycle. That plague in Kenya can be more widespread than previously thought was shown by a survey in the Tana River area prior to the construction of a dam at that site. Four of the seven species of rodents captured (*T. robusta*, *A. niloticus*, *L. striatus* and *Pterodromus tetradactylus*) were positive for plague.

Xenopsylla cheopis, *X. braziliensis* and *Dinopsyllus lypus* are abundant on the most important rodent reservoirs of plague in Kenya and, as elsewhere in East Africa, are the main vectors of the infection.

Tanzania (35,36,37)

In Tanzania the most important commensal and peridomestic rodents involved in the transmission of plague are *R. rattus* and *M. natalensis*. *Cricetomys gambianus*, *Lophuromys flavopunctatus*, *Tatera robusta*, *Otomys angoniensis*, *Arvicanthis niloticus* and *A. abyssinicus* are also involved where human cases occur. In most of the plague-endemic areas of the country, the majority of the rodents are *A. abyssinicus* and *M. natalensis*. *Lemniscomys striatus* has been found positive for plague in the Mbulu focus. *Lophuromys flavopunctatus*, *L. sikapusi*, *Otomys angoniensis*, *Pelomys fallax*, *O. denti* and *Gramomys dolichurus* are among other rodent species found positive for plague in a serological survey in the western Usumbara mountains. Once surveyed, plague will probably be found to be endemic in still other areas of the country and in other species of rodents. Reservoir species are widespread and human cases of plague occur in the country nearly every year.

Xenopsylla cheopis and *X. brasiliensis* are common on both *Rattus* and *T. robusta*. *P. irritans* has also been found frequently in the plague-endemic area of Lushoto (38). *X. brasiliensis* and *D. typhus* are more common than *X. cheopis* on rodents in the country (39). *X. humilis* and *X. nilotica* are found on *Tatera* and *Gerbillus* species (40).

Mozambique (41,42,43)

Mastomys natalensis is widespread in Mozambique as well as in neighbouring countries and is probably the main sylvatic reservoir of plague. In the cities, population densities of *R. norvegicus* and *R. rattus* are high and plague may have spread from *M. natalensis* to *R. rattus* in the 1976 outbreak.

Madagascar (41,44,45)

An estimated 15% of the island of Madagascar is endemic for plague and there is some evidence that strains of *Y. pestis* have become more virulent. The infection established itself on the high plateau of central Madagascar in 1921, remaining endemic and spreading over the years with the occurrence of sporadic cases. There are two large foci in the country: the first from the central province of Tananarive to the south in Fianarantsoa; the second in the north near the region of Balanana.

The only apparent reservoir of plague in Madagascar is *R. rattus*. The number of rodent species on the island is relatively small, with only three muroid rodents: *R. norvegicus*, the only species found in the ports and the most common species in the city of Antananarivo; *Mus musculus*, which is found everywhere but appears to have no role in the epidemiology of plague; and *R. rattus*, whose density is often high and is widely distributed in rural areas, rice fields, villages and urban areas. The flea vector is mainly *X. cheopis* but *R. rattus* is frequently parasitized by *Synopsyllus fonquerniei*.

Plague foci of central Africa

In central and southwest Africa, plague is endemic in Angola, Equatorial Guinea and the Democratic Republic of the Congo. Little information is available on the reservoirs and vectors in Angola or Equatorial Guinea.

Democratic Republic of the Congo (46,47)

Extensive studies have been carried out on the rodent reservoirs of the two plague foci in the Democratic Republic of the Congo. The areas have a rich rodent fauna and the main species involved in the

epidemiology of plague are *Arvicanthis abyssinicus*, *M. natalensis*, *Lemniscomys striatus*, *R. rattus* and *Leggada minutodites*, which continue to maintain plague transmission in the northeastern part of the country. *A. abyssinicus* is a peridomestic species which serves as an intermediary between the wild or sylvatic reservoirs and domestic species. *M. natalensis* is frequently found nesting in thatched roofs.

P. irritans is a possible vector of plague in the Democratic Republic of the Congo (46) and Angola, at least in domestic transmission (17).

The fleas *Dinopsyllus lypus* and *Ctenophthalmus cabirus* and *C. phyrus* are common on *Arvicanthis* and *Lophuromys* and have been found plague-positive, especially in the Blukwa plague focus. In the Lake Edward focus in the Democratic Republic of the Congo, *R. rattus* and *M. natalensis* are the principal commensal and peridomestic rodents and *Xenopsylla brasiliensis* the most important flea vector.

The plague focus of northwest Africa

Mauritania (48,49)

A focus of plague exists in the northern part of western Mauritania. The rodent populations of the area, particularly the gerbils, *Gerbillus gerbillus* and *G. nanus*, the jerboa *Jaculus jaculus* and *Psammomys obesus* are important desert or semi-desert rodent species. The gerbils are the principal reservoirs of plague in the area.

Xenopsylla ramesis is the vector among the *Psammomys* populations. *X. nubica* is common on gerboas *Jaculus jaculus*. *Synosternus cleopatrae* is the most common flea on *Gerbillus* species and is the vector of plague among gerbil populations. *X. cheopis* is found only in seaside towns. All these species feed readily on humans and can transmit *Y. pestis* from rodent reservoirs to domestic animals and humans.

The plague focus of North Africa

Libya (50,51)

Libya appears to be the only country in North Africa still endemic for plague. Though the focus was silent for some thirty years, cases appeared in the Nofila area in 1972. Surveys of rodents in the area indicate that *G. gerbillus* and *Meriones shawi* are the most common species of rodents in areas where human cases of plague have been reported. The former were captured inside the tents of nomads and may serve as maintenance host for the infection. *M. libycus* is an even more widespread

species and is comparatively resistant to plague; it was also found to be seropositive for plague in Libya. Other animals, including camels, may also be involved in the epidemiology of plague. Further investigation is necessary for a better understanding of the reservoirs maintaining plague in this long-standing focus.

Flea densities are low in the Libyan plague foci. In the northern plague foci, *M. libycus*, *M. caudatus*, *M. shawi* and *P. obesus* are present. The flea ectoparasites are *X. ramesis*, *X. cheopis*, *X. taractes* and *Nosopsylla henleyi*.

The plague focus of the Arabian Peninsula

Yemen (52)

A small outbreak of plague occurred in Yemen in 1969 in a focus in which earlier outbreaks had occurred at the beginning of the century and in 1951 and 1952. Epidemiological investigation following the 1969 outbreak showed *R. rattus* present in houses, and *Meriones rex* and gerbils (*Gerbillus* species) in the fields surrounding the infected village, although none were found infected with *Y. pestis*. No information is available on the flea vectors in this focus nor on its current status.

Plague foci of southwestern Asia

Islamic Republic of Iran (2,53)

Though no human cases have been reported for many years, there are three active areas of endemic plague still known to exist. These are Kordestan (Kurdistan) and Hamadan in the west, and a focus in East Azerbaijan (including the Sarab desert) in the northwest. Prior to its discovery in 1980 plague had never been reported from this area. The other foci have been known for a long time and are well studied. The most important rodent reservoirs in the area are the gerbils *M. libycus* and *M. persicus*, both of which are highly resistant to plague infection, and *M. tristrami* and *M. vinogradovi* which are highly susceptible to both infection and the disease. *Tatera indica* has also been associated with transmission of *Y. pestis* in the country.

The flea vectors among the gerbils are *Xenopsylla buxtoni* and *Stenoponia tripectinata*. Flea densities are often high on *M. persicus*. Past epidemics of bubonic plague may have been due to human-to-human transmission by *P. irritans*.

Plague foci of the Russian Federation and the CIS Republics (54,55,56,57,58,59,60)

The endemic foci of plague cover vast areas and their ecology, reservoirs and vectors differ considerably from one another. They will therefore be considered separately based on a report by B.K. Fenjuk and V.P. Kozakevic to WHO, 1968 (unpublished report). An extensive review of the plague literature in the former USSR was made by Pollitzer in 1966 (54). The classification of these foci are taken from that report.

A large natural focus of plague remains active in the Asian part of the Russian Federation and in the Asian republics. In the pre-Caspian region, the main rodent reservoir of plague is the suslik, *Citellus pygmaeus*. In sandy areas, *Meriones meridanus* (a species rather resistant to plague infection) and *M. tamariscinus* may also be reservoirs. In the central Asian plague focus, the main rodent reservoirs in the desert lowlands are *Rhombomys opimus* and *Meriones erythrorus* and in the high mountain areas of this large focus, the marmots *Marmota baibacina* and *M. caudata*. In the transcaucasian area, gerbils (*M. libycus* and others) are important reservoirs, while *Marmota siberica* and *Citellus dauricus* are involved in the epidemiology of plague in the Transbaikalian focus. Commensal rodent species have rarely been involved in plague transmission in these foci.

The northwest Caspian focus

The focus covers an area lying to the west of the lower source of the Volga and the northern shores of the Caspian Sea. The western boundary of the focus is the River Don. Enzootic plague is reported to have disappeared from a large portion of this focus. The main reservoir of plague is the small or lesser suslik, *Citellus pygmaeus*. Two species of voles, *Microtus arvalis* and *laagers* may have been involved as reservoirs in the focus (61).

The most important flea vectors are *Ceratophyllus tesquorum* and *Neopsylla setosa*.

The focus between the Rivers Volga and the Ural Mountains

Two types of landscape are found in this area: rocky steppes in the north, west and east; and sandy semi-desert (the Volga-Ural sands). The main reservoir of plague in the steppes is the small suslik, *C. pygmaeus*. In the sandy areas it is the gerbil *Meriones meridianus* and to a lesser extent *M. tamariscinus*.

The most important flea vectors in the steppe regions are *Ceratophyllus tesquorum* and *Neopsylla setosa* and in the sandy semi-deserts, *Xenopsylla conformis*, *Ceratophyllus laeviceps* and *Rhadinopsylla cedevis*.

The focus on the left bank of the Ural River

The reservoirs in this area are also *C. pygmaeus* and *M. tamariscinus*. The flea vectors are the same as those mentioned above.

The focus in the Transcaucasian lowlands

This focus in Azerbaijan may be linked with the natural focus in Iranian Kurdistan. The main plague reservoir in this area is the gerbil, *Meriones libycus erythraeus*. The flea vectors are *X. conformis* and *C. laeviceps*.

The focus in the high mountain areas of Transcaucasia

This focus of plague is located at an altitude of 2000 to 3000m and covers areas in Armenia and Azerbaijan. The main reservoir species is the vole *Microtus arvalis*; infected vole fleas *Ctenophthalmus teres*, *C. wladimiri* and *Ceratophyllus caspius* have been found in nature. The identity of the main rodent reservoir in the lower altitudes and plains of this focus remains uncertain.

The central Asian desert focus

This focus covers a large area of central Asia and southern Kazakhstan Republic to the borders with China in the east and with Afghanistan and Iran in the south. The most important reservoir is the gerbil, *Rhombomys opimus*.

The flea vectors are *Xenopsylla skrjabini*, *X. hirtipes*, *X. gerbilli gerbilli*, *X. gerbilli minax*, *X. gerbilli caspica*, *X. nuttali* and *X. conformis*.

The Tian-Shan focus

This focus is situated in a mountainous area of Kazakhstan and Kirgasia. The main reservoir is *Marmota baibacina* and the flea vectors are *Oropsylla silantiewi* and *Rhadinopsylla ventricosa*.

The Pamir-Alai focus

This is a focus of limited size in the Alai valley. The reservoir is the Altai marmot, *Marmota caudata*. The flea vectors are *R. ventricosa* and possibly *O. silantiewi* and *Ceratophyllus lebedwi*.

The Transbaikalian focus

This is a focus on the north-east edge of the extensive Mongolian focus of plague. The rodent reservoirs are *Marmota sibirica* and *Citellus dauricus*. The main vector flea is *Oropsylla silantiewi*. Isolations of *Y. pestis* have also been made from the flea *Frontopsylla luculenta*.

The High Altai and Tuva Autonomous Region focus

In this area, also adjacent to Mongolia, the weasel *Putorius eversmanni* and the suslik *Citellus undulatus* have been found plague-positive. The fleas on the suslik species are *Ceratophyllus tesquorum*.

Plague foci of southeast Asia and the western Pacific

India (62,63,64,65,66,67)

A large number of rodent species are known from the Indian subcontinent, including some 46 genera, 135 species and many subspecies. The diverse ecological conditions in different parts of this large country has also resulted in a diverse rodent and flea ectoparasite fauna. Rodents cause serious agricultural and stored food losses and are important reservoirs of a number of diseases including plague, leptospirosis and murine typhus. Many species of rodents have been reported as actual or potential reservoirs of plague. Depending on the region, the more important species are *Bandicota bengalensis*, *Tatera indica*, *Rattus norvegicus*, *R. rattus* and *R. rattus diardii*, among others.

The species shown to be important as reservoirs of plague at one time or another include the urban rats, *R. rattus*, *R. norvegicus* and *B. bengalensis*; the latter is also an important agricultural pest. The gerbil *Tatera indica*, the Indian field mouse *Mus budooga*, and the squirrels *Funambulus pennanti* and *F. palmarum* have all been found positive for plague in various foci.

Until the recent outbreak of plague in Maharashtra and Gujarat States of India in 1994, no human cases of the disease had been reported since the cases in Karnataka State in 1966. However, there have been a number of suspected outbreaks reported including in Himachal Pradesh in 1983, similar to pneumonic plague (22 cases, 17 deaths).

From the 1960s to 1989, a total of 188,025 rodent sera were examined in India. Only 12 sera from *Tatera indica* were found positive for *Y. pestis* antibody in 1979 and three from the same species found positive in 1989. Only two *R. rattus* were reported as serologically positive for

Y. pestis in 1988 despite many reports of rat falls from the country. Population densities of rats including *B. bangalensis*, *R. norvegicus* and *R. rattus* in most urban areas are generally high. In rural areas agricultural development, including large irrigation projects, is changing ecological patterns and the composition of rodent populations.

As of 1973, 76 species of fleas have been recorded in India (68). The most important rat flea vector of *Y. pestis* in urban or domestic situations (found on wild rodents) is *X. cheopis*, while *X. astia* predominates on wild rodents. *X. brasiliensis* is also frequently found on rodents. *Nosopsyllus faciatus* has also been found infected by *Y. pestis*.

Nepal (69)

Only a few cases of plague have been reported from Nepal and little information is available on the reservoirs. During a small outbreak in 1971, *P. irritans* was reported to be the vector in the affected village.

Myanmar (4,70,71,72,73,74,75,76)

Zoonotic plague is endemic over large areas of the country. The rat species with the highest plague antibody rates in Yangon (Rangoon) among 1,620 animals tested in 1976 was the bandicoot *B. bengalensis*, the most common rodent species in the city. Its rate of positivity was 15.4%. *R. norvegicus* showed 11.1% positivity, *R. rattus* 7.6%, and the insectivore *Suncus murinus* 3.35%. Plague antibody in *B. bengalensis* is transient in nature and when found indicates recent infection. Little is known, however, about the epidemiology, maintenance cycle or reservoirs of plague in the rural or sylvatic areas of the country.

Xenopsylla cheopis and *X. astia* have been recovered from the three species of *Rattus* as well as from *B. bengalensis* and the shrew *S. murinus* in Yangon (Rangoon). *X. astia* is most abundant on the bandicoot and Norway rat while *X. cheopis* is more common on *R. exulans* and *S. murinus*. Both species of *Xenopsylla* are found in almost equal numbers on *R. rattus*. The two species of *Xenopsylla* are probably the most important vectors of both plague and murine typhus (75). *R. rattus* has been considered the most important reservoir of plague in the foci in the country and *X. cheopis* the most important vector with *X. astia* also a vector (76).

Indonesia (77,78,79,80)

A focus of plague was active until recently in the Boyolali area of central Java. There have been no recent reports of plague activity in this focus despite an active surveillance programme. The two rodent species

from which *Y. pestis* was detected in this area are *R. rattus diardii* and *R. exulans ehippium*. *R. r. diardii* is the predominant species inside houses and *R. exulans* is the most common species in the fields.

The most common flea species and vectors of plague in the Boyolali focus are *X. cheopis* and *Stivalis cognatus*. *R. rattus* and *X. cheopis* have been collected most often from buildings, where contact with humans occurs readily. *R. exulans* and *S. cognatus* have generally been taken in field and forest habitats.

Viet Nam (81,82,83,84,85,86,87,88,89,90,91,92)

In urban areas, the reservoirs of plague are the domestic rats *R. norvegicus* and *R. rattus* and the insectivore *S. murinus*. Sylvatic plague was first found in Viet Nam in 1968 when specimens of the large bandicoot *B. indica* and the fleas (*X. cheopis*) infesting it collected near a plague focus were found positive for plague. Recent studies indicate that plague is probably maintained by these species in a domestic or peridomestic cycle and it is doubtful that there is a true sylvatic cycle in the country (90).

Only *X. cheopis* was collected on all four species of small mammals trapped in the Pleiku plague-endemic area: *R. rattus*, *R. norvegicus*, *B. bengalensis* and *S. murinus*. The species *R. rattus*, *R. norvegicus* and *S. murinus* are most closely associated with plague transmission. Of the fleas collected on four small mammal species in Pleiku, 94% were on *R. rattus* (91). *X. cheopis* was the most common flea species collected on small mammals in a plague focus; *X. vexabilis* was found in much smaller numbers (92). It thus seems likely that the most important flea vector of plague in the country is the Oriental rat flea, *X. chopis*. *B. indica* has also been found plague-positive in Viet Nam, infested with *X. cheopis* (85).

China (74,93,94,95)

China is the only country of the western Pacific region aside from Viet Nam where plague remains endemic. There are ten geographical foci of plague in China. The following review of the status of plague in these foci is taken from a report provided by Xu Rong-man (94). Foci are classified according to rodent reservoir species.

- (1) The plague focus of the commensal rat *Rattus flavipectus*. This species is found in southern Yunnan and the coastal areas of Zenjiang, Fujian, Taiwan, Guangdong and Guangxi in southern China, an area of over 20 000 sq. km which includes

56 counties. Other hosts infected with *Y. pestis* in these regions have been *R. norvegicus*, *M. musculus* and *Suncus murinus*. The only part of this area where human plague cases have been reported since 1953 is southern Yunnan.

- (2) The plague focus characterized by *Eothenomys miletus* is located in the mountains of northwestern Yunnan over an area of 600 sq. km. The main vectors are *Ctenophthalmus quadratus* and, to a lesser degree, *Neopsylla specialis*. The main reservoir host is *Eothenomys miletus*. *Apodemus chevrieri*, *Apodemus speciosus* and *Rattus nitidus* have also been found infected in the focus. While enzootic plague has been reported on many occasions, no human cases have been reported.
- (3) The *Marmota himalayana* plague focus. This large focus is found mainly in Tibet and Qinghai, south to the Himalaya Mountains, north to the Qilian mountains in Xinjiang and east to southern Gansu, covering nearly 1 000 000 sq. km of land and 54 counties. The principal flea vectors are *Callopsylla dolabris* and *Oropsylla silantiewi*. Other fleas and hosts found infected are *Rhadinopsylla li* and *Pulex irritans*, *Ochotona daurica annectens*, *O. curzoniae*, *Lepus oiostolus*, *Vulpes ferrilata*, *Procarpra picticauda*, *Mus musculus*, *Cricetulus migratorius*, *Microtus oeconomus* and *Pitymys leucurus*. This stable enzootic focus is active from April to September. It is the most important focus of plague in China and the majority of human cases in the country arise from this focus.
- (4) The *Marmota caudata* plague focus is in southwestern Xinjiang. It is part of the Pamir Plateau plague focus in Middle Asia and covers 600 sq. km in two counties. The main vectors are *Oropsylla silantiewi* and *Rhadinopsylla li*. *Citellophilus lebedewi priceps* has also been found infected, as has the rodent *Pitymys juldaschi*. There have been no human cases of plague recorded in this zoonotic focus.
- (5) The *Marmota baibacina* and *Spermophilus undulatus* focus. Located in the Tianshan Mountains of Xinjiang Province, the focus covers an area of 7,000 sq. km over 10 counties, extending into Kazakhstan and Kyrgyzstan. The main flea vector is *Oropsylla silantiewi*. *Callopsylla dolabris*, *Citellophilus tesquorum altaicus* and the widespread *Clethrionomys glareolus* are other rodents that have been reported as infected in the focus. Epizootic plague occurs from May to September. No human cases have been reported in this focus since 1973.
- (6) The *Spermophilus alaschanicus* plague focus in Gansu-Ningxia covers eastern Gansu and southern Ningxia in northern China,

an area of 3,000 sq km over five counties. The main flea vector is *Citellophilus tesquorum mongolicus*. *Neopsylla abagatui*, *Frontopsylla elata* and *Ophtalmopsylla praefecta* are also found infected with *Y. pestis*. Other mammal species infected are *Myospalax fontanieri*, *Meriones meridianus*, *Cricetulus triton*, *Allactaga siberica* and *Ochotona daurica*. Epizootic plague occurs from April to October. No human cases have been reported since 1978.

- (7) The *Meriones unguiculatus* plague focus in the Inner Mongolian plateau covers the Inner Mongolian plateau and the three nearby Provinces of Ningxia, Shaanxi and Herbei, an area of 100 000 sq km. The principal flea vectors are *Nosopsyllus laeviceps* and *Xenopsylla conformis*. *Neopsylla pleskei*, *Citellophilus tesquorum mongolicus*, *Paradoxopsyllus kalabukovi*, *Rhadinopsylla insolita* and *Rhadinopsylla tenella* have also been found infected. Other mammals found infected in the focus are *Spermophilus dauricus*, *Spermophilus erythrogenys*, *Meriones meridianus*, *Dipus sagitta* and *Mus musculus*. Epizootic plague occurs from April to November; there have been no human cases reported since 1973.
- (8) The *Spermophilus dauricus* plague focus in the plains of the Songhuajiang-Liaohe Rivers includes parts of Inner Mongolia, Liaoning, Jilin and Heilongjiang provinces over an area of 120 000 sq. km. The main vector is *Citellophilus sungaris*; *Neopsylla bidentaformis* and *Xenopsylla cheopis* are also involved. Rodent reservoirs are *R. norvegicus* and *M. musculus*. No human cases have been reported since 1959.
- (9) The *Microtus brandti* focus on the Xilin Gol Plateau covers 60,000 sq. km. in northern Inner Mongolia. The main vectors in this purely zoonotic focus are *Amphipsylla primaris* and *Neopsylla pleskei* along with *Frontopsylla luculenta*, *Neopsylla bidentaformis*, *Citellophilus tesquorum mongolicus* and *Nosopyllus laeviceps*. *Meriones unguiculatus*, *Spermophilus dauricus*, *Ochotona daurica*, *Allactga siberica* and *Mus musculus* are rodent species found infected.
- (10) The *Marmota bobac siberica* focus in the Hulum Buir Plateau. This epizootic focus covers 40 000 sq. km. in northeastern Inner Mongolia and is part of a focus with the same reservoir in the Russian Federation and Mongolia. No isolation of plague has been made from marmots or their fleas for many decades.

Plague reservoirs of North America

United States of America

96,97,98,99,100,101,102,103,104,105,106,107,108,109)

Plague infection has been found in many different animal species in North America. During a period of active surveillance in 1970-1980, evidence of plague infection was found in 76 species of five mammalian orders. Most of the wild-rodent-associated plague cases in the United States are reported in the south west, including most of New Mexico, northeastern Arizona, southern Colorado and southern Utah. The major hosts of *Y. pestis* in this area are the prairie dog *Cynomys gunnisoni* and the rock squirrel *Spermophilus variegatus*. Devastating plague epizootics are common among prairie dog populations in the large colonies formed by these species. Epizootics among *C. gunnisoni* may kill 99% of the colony and it may take four to five years for the affected colony to recover. Despite the heavy mortality, survivors are found with antibody to plague. Human cases acquired from prairie dog sources are relatively few.

Similar epizootics have been observed among *C. ludovicianus*, *C. leucurus*, and *C. parvidens*. More than 80% of the cases of wild rodent-associated human plague in the United States occur in this area and are associated with these host-flea complexes. Despite the size of epizootics, human cases are relatively few and generally result from contact with an infected animal rather than from the bite of the *Opisocrostis* species, which do not readily bite humans.

On the Pacific coast the reservoirs are *Spermophilus beecheyi* (the most important rodent species in the epidemiology of plague on the Pacific coast), and the chipmunks *Eutamias* species, *Microtus californicus* and *S. lateralis*. There has been a single report of an epizootic in the domestic fox squirrel, *Sciurus niger*, in Colorado state. In the northern foci of plague ground squirrels, including *S. beldingi*, are important reservoirs. Other rodent species are frequently infected and there has been a report of the black footed ferret *Mustela nigripes* found infected with plague in Wyoming which endangers the only known colony of this species. Cats have frequently been a source of commensal infection in the southwestern United States. Several cases of plague have been contracted directly from domestic cats, *Felis catus*, infected after contact with plague-infected rodents. The flea vectors of plague in the southeast are *Opisocrostis hirsutus* and *O. tuberculatus* on the prairie dog *C. gunnisoni*, and *Diamanus montanus* and *Hoplopsyllus anomalus* on the rock squirrel *S. variegatus*.

Rapid human population growth and rural development have increased the densities of *Spermophilus variegatus* populations by providing additional habitats. Plague cases in California generally originate from two primary epizootic complexes: *S. beecheyi* and its fleas *D. montanus* and *H. anomalus*, and a less well-defined complex involving several species of chipmunks, *Eutamias* species and the golden-manteled squirrel *S. lateralis*.

The host-flea complexes involved in the transmission of *Y. pestis* both in zoonotic and reservoir-to-human transmission are summarized in Table 4.

Plague foci of South America

Bolivia (3,110)

Since the first reports of plague in Bolivia in the early 1920s, plague has spread widely throughout the country. Today there are two widely-separated foci, one in the north-west near La Paz, the other in south central Bolivia. When plague outbreaks occur in settled areas the rodent involved is usually *R. rattus* and the vector flea *X. cheopis*. In sylvatic areas in Vallegrande Province, *Graomys griseoflavus* and *Galea musteloides* have both been found infected with plague. *G. griseoflavus* is particularly important, as it frequently infests domestic areas and transmits plague to purely sylvatic rodent populations. Other rodents found infected with plague in Bolivia are *Dasyprocta variegata boliviae*, *Hesperomys fecundus*, *H. venustus*, *Oryzomys flavescens*, *Oxymycterus paramensis*, *Phyllotis wolhshohni*, *Rhipidomys leucodactylus* and *Sylvilagus brazilensis gibsoni*. More research is needed to clarify the relative importance of each of these species in the sylvatic foci.

Brazil (3,111,112,113)

Plague apparently entered Brazil by sea route in 1899, infecting first Santos and then Sao Paulo. Plague has spread to other ports and to rural areas of Brazil; while the infection has disappeared from Sao Paulo several natural foci have become established in the country. Of the commensal reservoirs of plague, *R. rattus* is the most important. In the plague foci which persist in northeastern Brazil, the most important wild rodent reservoir is *Zygodontomys lasiurus pixuna*. The cavia species *Galea spixii*, *Cercomys inermis*, *Holochilus sciureus*, *Kerodon rupestris* and *Cavia aperea* are among the species that have been found naturally infected with plague. Plague-infected fleas have been found on *Calomys callosus* and *Oryzomys subflavus*.

Table 4 List of host–flea complexes found involved in epizootic plague amplification in western North America by geographic regions

States & regions	Rodent species	Flea vectors
Arizona, New Mexico so. Colorado, so. Utah	<i>Spermophilus variegatus</i>	<i>Diamanus montanus</i> <i>Hoplopsyllus</i>
Arizona, New Mexico Colorado, Utah, Rocky Mts and west	<i>Cynomys gunnisoni</i>	<i>Opisocrostis hirsutus</i> <i>O. tuberculatus</i> <i>cynomuris</i>
Colorado (east of Rocky Mts) western Texas, Oklahoma, Kansas	<i>C. ludovicianus</i>	<i>O. hirsutus</i> <i>O. tuberculatus</i> <i>cynomuris</i>
Wyoming, north-western Colorado, north-eastern Utah (high plains grasslands)	<i>S. richardsoni</i>	<i>O. labis</i> , <i>Oropsylla idahoensis</i> (Rocky mts) <i>O. t. tuberculatus</i> , <i>Thrassis bacchi</i>
California, Oregon, northern Nevada, Southeastern Idaho (montane meadows, great Basin sagebrush-grasslands)	<i>S. beldingi</i>	<i>Thrassis francisi</i> , <i>T. pandorae</i> , <i>T. petiolatus</i> <i>Opisocrostis t.</i> <i>tuberculatus</i>
Southern Idaho, eastern Oregon, Nevada, Utah, (Great Basin, sagebrush)	<i>S. townsendi</i>	<i>T. francisi</i>
Idaho, Utah, Wyoming (Great Basin & mountain 4000-8000 elevation)	<i>S. armatus</i>	<i>T. pandorae</i> <i>T. francisi</i>
California, Oregon, western Nevada (valleys, foothill savanna, open pine forest to temperate rain forest edge)	<i>S. beecheyi</i>	<i>D. montanus</i> <i>H. anomalus</i>
Arizona, California, Colorado Idaho, Montana Nevada, New Mexico, Oregon (mountain areas, open pine forest)	<i>S. lateralis</i>	<i>Oropsylla idahoensis</i> <i>D. montanus</i> (Sierra-Cascade, <i>O. labis</i> (Rocky mountains)
Western United States from Rocky mts westward <i>M. eutamias</i> , <i>M. eutamias</i> , <i>M. eutamias</i>	<i>Eutamias spp</i> ^a 16 species	<i>Monopsyllus eumolpi</i> , <i>M. ciliatus</i> , <i>M. fornacis</i> (last 3 from Pacific states only)
Western USA from Texas to the Pacific States (desert to high Montana shrubby habitats)	<i>Neotoma spp</i> ^b 8 species	<i>Orchopeas sexdentatus</i> <i>O. neotomae</i> <i>Anomiopsyllus spp</i>
Colorado, Wyoming California (urban residential and rural environments) States.	<i>Sciurus niger</i> ^c	<i>Orchopeas howardii</i>

a Individuals of nine species found plague infected or carrying plague-infected fleas

b Individuals of five species were found to have been plague-infected or carried plague-positive fleas

c This peridomestic species introduced in western cities as a park squirrel with *O. howardi*
source: Barnes, A.M. (1982) Surveillance and Control of Bubonic Plague in the United States. Symp.Zool. Soc. London,
50:237-270.

Several species of fleas found on wild hosts in northeastern Brazil and the State of Bahia may be involved in the maintenance and transmission of plague, particularly fleas of the genus *Polygenis*. Of these *P. bohlsi jordani* has perhaps the widest distribution, highest density and greatest contact with domestic rats followed by *P. tripus*.

Further to the south in the plague-endemic area of Goiás 14% of the *O. elurus* and *Calomys callosus* have been found infested with *P. bohlsi*. The infestation rate for *Zygodontomys* sp. has been reported at 42%. Still further south in the focus of Minas Gerais, the infestation rates of *P. tripus* were 50% on *O. subflavus*, 47% on *Z. lasiurus* and 30% on *R. norvegicus*.

Ecuador (115,116)

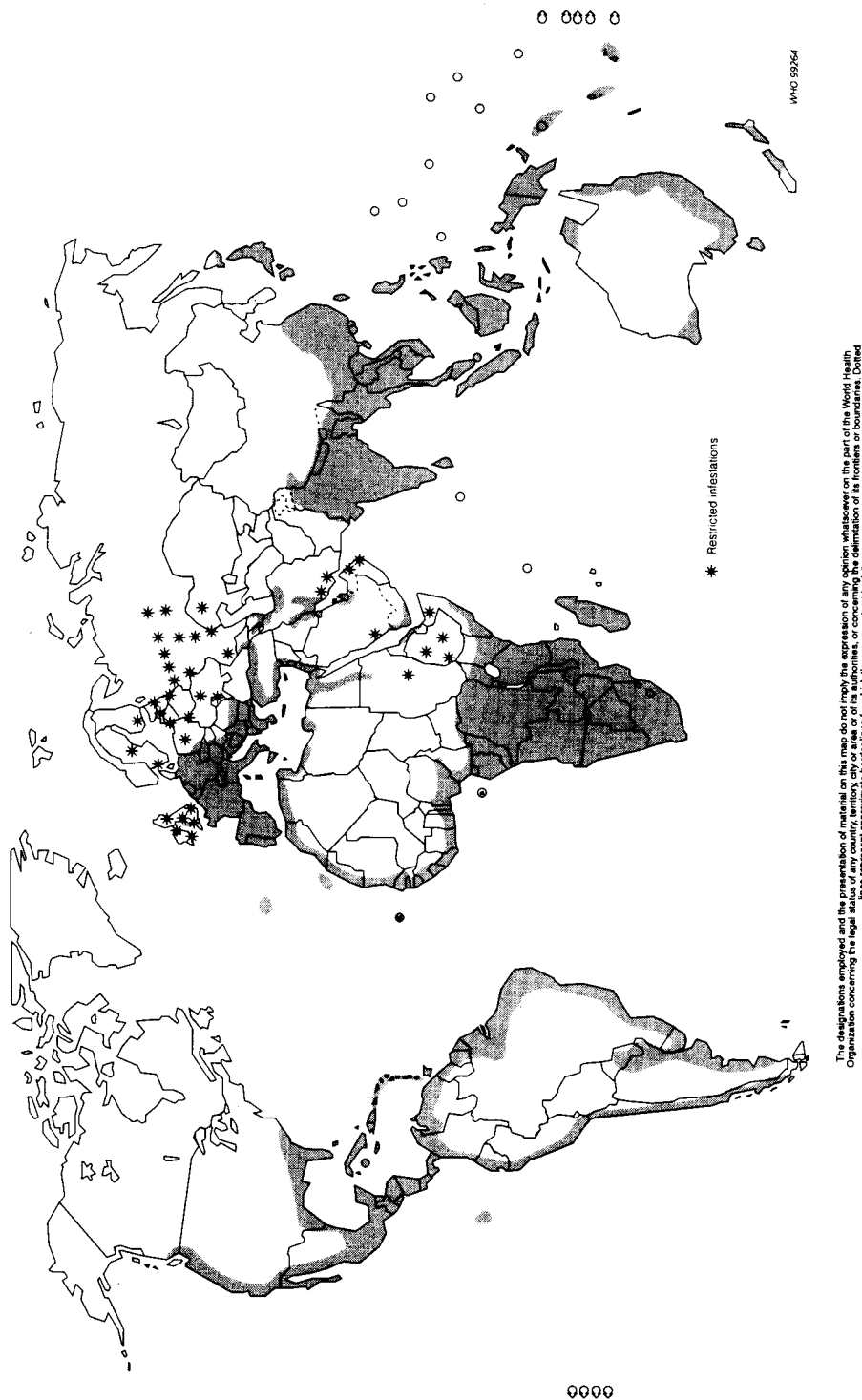
Rattus norvegicus, *R. rattus* and their common flea ectoparasite *X. cheopis* are found in most of the towns of the coast of Ecuador. However, the *Rattus* species appear to have little role in the transmission of plague in the country. Domesticated guinea pigs are frequently infected and pass the infection on to humans. The specific flea of the guinea pig, *Tiamastus cavicola*, has been found naturally infected with plague (116). Guinea pigs are often infested with *P. irritans* though their vectorial role is uncertain. The most common wild rodents in some areas of plague outbreaks are *Akodon mollis* and *Oryzomys xanthaeolus*. These species have been found infected with plague inside houses. *Sigmodon peranus* and *S. puna* have also been found naturally infected with plague. The squirrel *Sciurus stramineus nehouxi* is considered a reservoir in Loja province as it is comparatively resistant to plague and is responsible for acute epizootics in the highly plague-susceptible *A. mollis* and *O. xanthaeolus*. *Polygenis litargus* is one of the most important flea vectors of plague on wild rodents in Ecuador. The fleas *P. litargus*, *P. bohlsi bohlsi*, and *P. brachimus* infest the important reservoirs *Oryzomys xanthaeolus* and *Akodon mollis* in Loja province where *Sciurus stramineus* may be one of the wild-rodent plague reservoirs in this province. There is little information on the principal rodent reservoirs or flea vectors of plague in Tungurahua and Canar provinces, which also have foci of plague.

Peru (110,115,116,117)

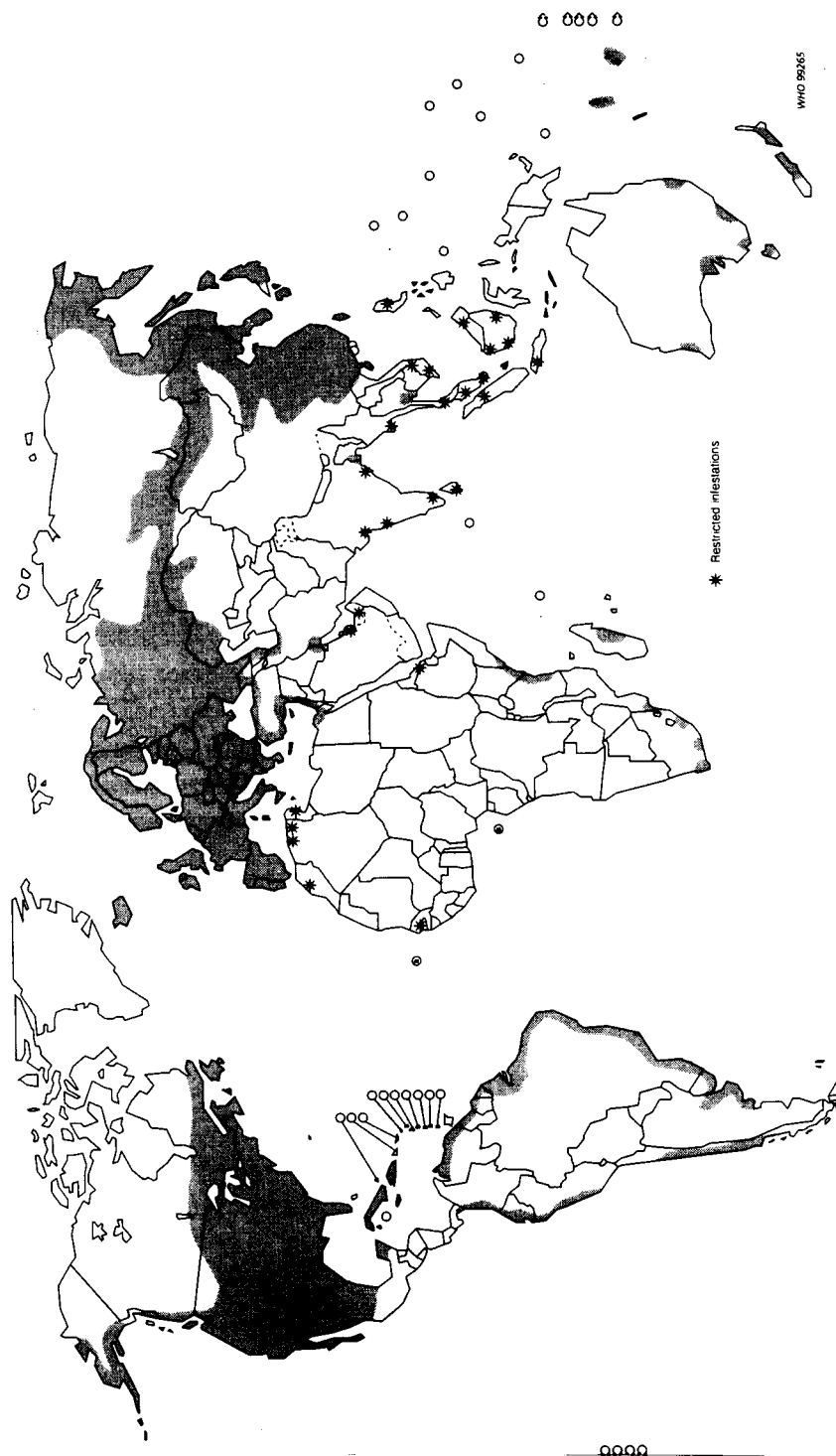
At the beginning of the century *X. cheopis* transmitted plague was introduced into populations of *R. rattus* and *R. norvegicus* and subsequently wild rodent foci and epizootics developed on the Peru-Ecuador border and in the Andean district of Huancabamba. The principal reservoir in the Peru-Ecuador border focus is the tree squirrel *Sciurus stramineus*, parasitized by the flea *Polygenis litargus*. In the Huancabamba district, the infection is carried mainly by

the mountain field mouse *Akodon mollis* and a oricetine rat, *Oryzomys andinus*. Other species of *Oryzomys* are associated with plague in the area as are the cavy *Cavia tschudii* and the cottontail rabbits *Sylvilagus andinus* and *S. ecaudatus*. The progenitor of the guinea-pig, *Cavia porcellus*, is frequently kept in houses in the area and is often infected by plague. *C. porcellus* and *C. tschudii* are parasitized by *Hectopsylla* species and *Tiamastus cavicola*, all of which have been found infected by plague in nature. In urban areas and the coastal cities, *R. norvegicus* and *R. rattus* are common and are parasitized by *X. cheopis*; this is the only important vector species when *Rattus* species are involved in plague transmission in settlements. While it appears that *A. mollis* and *Oryzomys xanthaeolus* are the most common sylvatic rodents and most frequently found infected with plague, many aspects remain to be clarified regarding the epidemiology of plague transmission in Peru, particularly those related to the wild rodent reservoirs.

Map 2 **Distribution of *Rattus rattus***



Map 3 Distribution of *Rattus norvegicus*



The designations employed and the presentation of material on this map do not imply the expression of any opinion whatsoever on the part of the World Health Organization concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. Dotted lines represent approximate border lines for which there may not yet be full agreement.

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