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PLAGUE FLEAS

WITH SPECIAL REFERENCE TO THE MILROY LECTURES, 1924.

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CONTENTS.

INTRODUCTION.

IN the Milroy Lectures for 1924, Lt-Col. W. Glen Liston gave an account of the growth of our scientific knowledge of the epidemiology of plague, to which he himself has contributed so much, first as an independent pioneer, and later as a member of the Commission for the Investigation of Plague in India.

The earlier work of the Commission showed conclusively that bubonic plague does not become epizootic among rats in the absence of rat fleas, and that the intensity of the epizootic increases with the number of fleas, and diminishes with rise of atmospheric temperature.

The later labours of the Commissioners were devoted to the investigation of the factors governing the spread of plague in India, and to the attempt to explain the remarkable anomalies in its distribution in such provinces as Madras, Eastern Bengal and the United Provinces.

As time went on it became evident that the spread of this deadly malady was by no means uniform throughout India. According to Norman White, at the end of twenty years, the incidence of plague mortality varied from 122·27 per 1000 of the mean population in the Punjab, and 87·35 for the province of Bombay, to 3·45 for Madras Presidency, and 1·49 for Bengal. Moreover, large tracts of country and great cities remained throughout comparatively immune from plague.

It is generally recognised that the spread of plague is influenced by a number of factors varying in importance according to circumstances. The Commissioners closely investigated the effect of local variations in the rat population; the susceptibility of the rats to plague infection; the number of fleas per rat, *i.e.* the flea-index; climate; means of communication; and exchange of merchandise between plague-infected and non-infected districts; the structure of human dwellings as affecting the shelter they afford for rats.

The relative immunity of some parts of Eastern Bengal and Assam may reasonably be attributed to the paucity of *Rattus rattus* in human habitations.

The climatic factor is extremely complex. The original experiments of the Commissioners on the effect of temperature on the transmission of plague by fleas were unfortunately made with a mixture in varying proportions of different species of rat flea. These experiments need to be repeated with pure strains of fleas. Nevertheless, it would seem to be established that fleas transmit plague less readily at temperatures over 80° F.

It has been proved that high temperature, especially when associated with low humidity, hinders the multiplication of rat fleas and reduces the average number found per rat. Martin and Bacot have shown that high temperature and dryness of the atmosphere independently shorten the length of life of fleas living apart from their host, and have produced evidence to show that this effect is particularly great on obstructed plague-infected fleas. The dryer and hotter the atmosphere becomes the shorter the distance plague fleas can be transported.

St John Brooks analysed the meteorological data of a number of localities in relation to plague. He came to the conclusion that plague cannot maintain itself in epidemic form when the temperature rises above 80° F. accompanied by a saturation deficiency of over ·30 of an inch.

The saturation deficiency is a measure of the additional vapour tension required to saturate the air at the temperature in question.

The long-continued immunity of the City of Madras from plague attracted the special attention of the Commission (1912). In spite of being in constant communication with heavily infected districts, Madras City has only suffered from one small outbreak in its outskirts, in 1905. The Commissioners (1915) note that, though more than 100 cases of plague are known to have entered the city, no epidemic developed in connection with them. Prof. Ashworth, commenting upon my researches on the spread of plague, in his address to the Zoological Section of the British Association, 1923, draws attention to the fact that in Madras City during the twenty-one years, 1897–1917, plague has occurred in twenty of those years, but the average mortality was only ·013 per thousand, that is, though the infection has been repeatedly introduced there, it failed each time to set up an epidemic.

The Commissioners found sufficient rats in the city to maintain an epizootic. These rats proved more susceptible to plague than those of any other part of India; it is the general rule that the longer a locality has suffered from plague and the more favourable the general conditions for plague infection the greater the degree of natural immunity found among the rats. The number of fleas per rat was also adequate. The housing conditions were not unfavourable to plague infection.

Moreover, the climate of Madras City during the months November, December, January and February, is similar to that of Bombay and Rangoon during the months when plague is at its maximum. Plague is prevalent in

Mysore, the source of plague infection in Madras, during the months of August to February inclusive. In the Seventh Report of the Plague Commission (1912) we find the following remark: "It seems likely that Madras has escaped plague because infection has been unable to reach there, or has met with some obstacle on arrival."

In a subsequent report (1915) the Commissioners considerably extended the scope of their inquiry in Madras.

As a result of an elaborate investigation of the climatic conditions in the Presidency as a whole, they attributed the comparative immunity from plague of certain parts, including Madras City, to the existence of a belt of low-lying hot dry plain between the infected areas and the more humid regions of the coast. They point out that plague is carried from place to place in the bodies of infected fleas, and that rat fleas speedily succumb to the combined effects of a high temperature and dryness.

In other words, they consider that the immunity of Madras City depends on climatic obstacles to the transference of infection, an attitude still endorsed by Glen Liston in his third Milroy Lecture.

In view of the evidence just presented that as a matter of fact plague infection has been almost annually transferred to Madras, and considering that a protracted epizootic among the rats has actually occurred in the outskirts of the city, it is difficult to understand how this attitude can be maintained. In my humble opinion the explanation put forward by the Commissioners of the immunity of certain parts of the Madras Presidency from plague must be rejected. Surely it seems more rational to seek the obstacle in the localities themselves. The climate of the Madras plains during the hot weather does undoubtedly afford a formidable obstacle to the transference of plague infection; but a critical examination of the data supplied by the Commissioners in Section LXXII of their report appears to me to show that in reality there is no serious obstacle to such transference during those months of the year when the disease is most prevalent in the infected regions. It must be remembered that a distance of only about 100 miles along a main line of railway intervenes between Madras City and centres in the foot hills where plague epidemics are liable to occur. Moreover, if fleas are transported on the bodies of infected rats and on the persons of human carriers they are to a great extent protected against the effects of adverse climatic conditions.

What, then, is the nature of the missing factor actually responsible for the mysterious immunity of several parts of India from plague?

The Flea Species Factor.

The Commissioners assumed, in the existing state of knowledge of the systemics of the Siphonaptera, that nearly all the fleas occurring on the rats of India belonged to one species, viz. *Xenopsylla cheopis*. A few cat and dog fleas were found on rats, a few *Xenopsylla scopulifer* are recorded from Poona, a small percentage of *Ceratophyllus fasciatus* were found during the winter months in the Punjab and the United Provinces. A few *Leptopsylla musculi* and *Pygiopsylla alladinis* were found in the Madras Presidency. Altogether they examined more than a million fleas.

In January, 1912, I made a collection of several hundred fleas from the rats of Colombo and sent them to Rothschild, who identified them as *Xenopsylla astia,* a newly described species never before found on rats. The following year I discovered that the rats of Madras City in India were also exclusively infested with *X. astia.* The Commissioners had previously examined 48,224 fleas from Madras City and identified them all as *X. cheopis.*

Up to that time Colombo had enjoyed an even more remarkable immunity from plague than Madras City itself. After drawing a comparison between the monthly mean temperatures and the relative humidity of Colombo and Bombay, I formed the opinion that the climatic conditions in Colombo during the months of December and January were not altogether unfavourable to the spread of plague.

This view was put forward in November, 1913. By the irony of fate, plague reached Colombo the very next month and has continued to recrudesce during the months of December and January ever since.

In the same paper I wrote as follows:

> No really satisfactory explanation has as yet been made of the remarkable freedom from plague of Southern India and Ceylon.... I venture to suggest that new light might be thrown on the epidemiology of plague by an investigation into the relative geographical distribution of *X. astia* and *X. cheopis* and into their relative capacity to act as porters of the plague bacillus under various climatic conditions, both between rat and rat, and between rat and man. It seems to me probable that both fleas will be found capable of conveying the virus of plague, but that under similar conditions *X. cheopis* will turn out to be a more efficient porter of infection than *X. astia.*

The theory has wide implications in plague epidemiology. Formerly the view prevailed that rat fleas were about equally efficient as transmitters of plague from rat to rat, but only those rat fleas which bite man readily need be considered in direct relation to the human epidemic. Most epidemiologists now admit that the marked variations in the bionomics and biting habits of rat fleas must effect their power of transmitting plague not only from rat to man, but also from rat to rat.

It is entirely a question of degree as between any two species of rat fleas.

In India we are concerned with the comparative transmitting powers of *X. cheopis* versus *X. astia* and *X. brasiliensis.* In Ceylon *X. cheopis* v. *X. astia,* in Japan *X. cheopis* v. *Ceratophyllus anisus,* in Australia and Marseilles *X. cheopis* v. *C. fasciatus* and *Leptopsylla musculi,* in Great Britain *X. cheopis* v. *C. fasciatus* and such fleas as *Ctenopthalmus agyrtes,* in Java *X. cheopis* v. *Pygiopsylla ahalae.* At Accra, West Africa, *X. cheopis* v. *X. aequisetosus* and *X. nubicus,* in Central Africa *X. cheopis* v. *X. brasiliensis.*

The genus Xenopsylla embraces an exceptionally wide range of species; some, such as *X. astia* and *X. nubicus,* are closely allied and liable to be

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confused; others, such as *X. cheopis* and *X. astia*, very different fleas and distinguishable at a glance.

I do not propose to enter here into a general discussion of the relative efficiency of all these fleas as porters of plague. Both experimental and epidemiological evidence point to the conclusion that both *Ceratophyllus fasciatus* and *X. astia* are less efficient as porters of plague from rat to rat than *X. cheopis*. Both these fleas bite man; *C. fasciatus*, according to Martin and Bacot, equally as well as *X. cheopis*; and *X. astia*, according to my own observations, somewhat less readily than *X. cheopis*.

If we accept the view that *C. fasciatus* is a relatively inefficient carrier of plague in nature, we have an additional explanation of the absence of severe plague epizootics among the rats of Western Europe. *R. norvegicus* appears to be the natural host of *C. fasciatus* just as *R. rattus* is that of *X. cheopis*. *X. cheopis* is still found in London, and was probably far more abundant in the days of the great plague when the houses of all London each harboured its colony of *R. rattus*.

My own observations have been made on *X. cheopis* and *X. astia*. I propose to deal particularly with the comparison between the relation of these two fleas to plague, which has special importance for India, Burma, Indo-China and Ceylon.

F. W. Cragg (1921) took up my suggestion for an enquiry into the geographical distribution of *X. astia* and *X. cheopis* in relation to plague. He published the results of the identification of 23,657 rat fleas from various parts of India in a series of papers.

Cragg was able to show that the localities where *X. cheopis* greatly predominated were particularly subject to severe plague epidemics. Taylor (1923) has pointed out that the converse is not equally true. While several large tracts of country where *X. astia* is almost exclusively found are practically immune from plague, there are exceptional instances where, according to Cragg's figures, a fairly heavy plague incidence is associated with a high percentage of *X. astia* and but few *X. cheopis*.

The results of single collections of rat fleas, however, may be most misleading, since they depend upon the season of the year, and the precise locality where the rats were caught. For example, a small collection of fleas from the outskirts of Colombo during the off plague season would probably show 100 per cent. *X. astia*, while a similar collection from the plague-infected zone in the heart of the city during the plague season might easily show over 50 per cent. *X. cheopis*.

India as a whole is too wide an area to exhibit the true relationship between the different species of rat fleas and plague, owing to the variety of other factors influencing the result in diverse regions.

Fully recognising this, Cragg was engaged upon a flea survey of an area in the Punjab especially chosen to throw light upon the problem, when he died a martyr to science at Lahore.

The climatic conditions, however, during the winter months in the Punjab are especially favourable to plague transmission by fleas. It is probable, therefore, that the correlation between *cheopis* prevalence and plague incidence is not so high in this part of India as in the more tropical regions.

While it is true that *X. astia* is, on the whole, more prevalent in the warmer and drier parts of India than *X. cheopis*, it is also evident that climate alone cannot account for the different distribution of these fleas.

I favour the view that *X. astia* was originally the indigenous rat flea of the plains of India, and that the tragedy of the spread of plague in India, as in Ceylon, Japan and Australia, followed upon the distribution of *X. cheopis* from the sea-board in merchandise, and the gradual extension of the area within which this flea is indigenous on rats.

As regards other parts of the world, I have been unable to trace any exception to the general rule that a large proportion of the rat fleas of all those localities where acute outbreaks of epidemic and epizootic plague are liable to occur are *Xenopsylla cheopis*.

The results of my earlier transmission experiments, together with Cragg's researches in India, established a *prima facie* case for my explanation of the relative immunity of certain parts of India from plague.

Glen Liston, however, in his Milroy Lectures, "hesitates to accept Hirst's explanation, especially as in my opinion sufficient evidence exists to show that the plague-free districts of the Madras Presidency owe their freedom from this disease to their climate. The nature of the climate at the same time serves to explain the presence of *X. astia* in these regions, for there can be no doubt that astia can thrive at atmospheric temperatures which are unfavourable for cheopis."

He seems to consider that the results of some experiments by Taylor and Chitre at Bombay indicate that the superior efficiency of *cheopis* over *astia* as a vector of plague is relatively slight.

I propose to deal with the salient points of these objections to my theory, and to endeavour to show that, while climate probably does exert an influence on the natural distribution of rat fleas, this factor is not so important in relation to plague as the artificial alterations in species distribution brought about by human agency.

Comparative Experiments on the Transmission of Plague by Rat Fleas.

An account of my earlier attempts (1914–15) to transmit plague by means of *X. astia* in Colombo, and my later comparative experiments with *X. astia* and *X. cheopis* has already appeared (1923).

I was led to the conclusion that *X. cheopis* was a much more efficient vector of plague than *X. astia*.

Further experiments with much larger numbers of fleas during the plague

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season, 1922–23, have not yet been reported in detail. As before, all attempts to transmit with *X. astia* were unsuccessful, though further positive results were obtained with *X. cheopis* under the same conditions; several *X. astia* were found to be "blocked" with growth of plague bacilli, but they could not be kept alive for long, or induced to bite a healthy animal.

Taylor and Chitre (1923) carried out a series of comparative experiments on the power of *X. astia* and *X. cheopis* to transmit plague between highly susceptible Madras rats and between guinea-pigs during the Bombay cool weather. Bombay rats have acquired a considerable amount of natural immunity to plague.

These experiments warrant the conclusion that *X. astia* can carry plague to extremely susceptible animals under favourable conditions, a result I anticipated ten years before in formulating my hypothesis.

Taylor and Chitre have devised a most useful new technique for separating mixtures of two species of flea, but their experimental methods are unsuitable for an accurate quantitative comparison between the transmitting power of two species of flea, both able to carry under the given conditions.

The results of Taylor and Chitre's series of experiments show that their method is not really quantitative. In the rat series the ratio of successful transmission with *cheopis* and *astia* was as 4 to 3; in the guinea-pig series as 8 to 1. *Astia* readily attacks and bites the guinea-pig and can easily be bred upon its blood. The difference in results does not therefore depend on the species of the rodent, but on some other factor or factors capable of affecting plague transmission in such experiments. Given highly susceptible animals, a virulent culture, and favourable climatic conditions, probably any rat flea could be made to transmit plague effectively in the laboratory, though it by no means follows it would play a significant part in the spread of plague in nature. In such comparative experiments, the two species of flea should be infected upon the *same* septicaemic rodent, separated afterwards, and the proportion of infective "blocked" fleas determined for each species, thereby eliminating marked variations in the degree of septicaemia and transmission by the indirect method. I have discovered a marked difference in the viability of male and female fleas captured from rats under Colombo conditions. It is therefore necessary to take the sex of the experimental fleas into account.

The detailed report of my 1923–24 experiments will show that *X. astia* can be made to carry plague in Colombo if the temperature is reduced to about 70° F. by surrounding the transmission chamber with an appropriate amount of ice and sawdust. In other words, if the climatic conditions are artificially altered to make them favourable to plague transmission.

I have recently succeeded in transmitting plague continuously to five rats in succession with the same batch of *X. cheopis* under particularly unfavourable climatic conditions in Colombo.

I have not obtained even one definite positive transmission with 596 *astia* in a series of 13 experiments at room temperature during four plague seasons in Colombo, though 132 *cheopis* under similar conditions have transmitted plague to 12 rodents in the course of six separate experiments.

It now remains to inquire into the origin of this difference in transmitting power. Light is thrown upon the problem by certain observations I have recently carried out on the relative frequency with which *astia* and *cheopis* bite the rat. I have obtained definite evidence that *X. cheopis* bites at considerably longer intervals than *X. astia*. Bacot has pointed out the effect that such a difference must have on the power of fleas to transmit plague.

Observations are still in progress on the comparative viability of unfed healthy fleas of the two species. So far I have been unable to detect any marked difference. During the cooler months of the Colombo year *cheopis* certainly lives at least as long as *astia*. The geographical distribution of the two fleas lends support to the supposition that *astia* is better able to resist the effects of an excessively hot and dry atmosphere, but the explanation may really be that *astia* spends more of its time on the body of the rat, where it would be protected to some extent by the exhalations of the rat from the drying effect of the air.

Astia seems to breed more readily than *cheopis* under unfavourable climatic conditions, but comparative experiments have not yet been carried out with a sufficient number of fleas.

Not only is *cheopis* naturally adapted to survive a longer interval between bites, but it bites more persistently than *astia*. More easily disturbed at the commencement of the act of biting, it returns vigorously to the charge again and again.

The "blocked" *cheopis* in one experiment must have survived at least 15 days at an average temperature of 85° F.

On the other hand, the only "blocked" *astia* I have so far been able to induce to bite a rat was kept in an ice box, except when under observation. More observations on the point are needed, but there seems little doubt that "blocked" *astia* have less vitality than "blocked" *cheopis* under unfavourable climatic conditions.

We have evidence, therefore, that rise of temperature does not exert an equal effect upon the plague transmitting power of different species of rat fleas.

As regards the transmitting power of *X. cheopis* compared with other species of fleas; Martin and Bacot working with *X. cheopis* and *Ceratophyllus fasciatus*, "gained the impression throughout our experiments that infection is more easily produced by *Xenopsylla cheopis*. The figures are too small to warrant this conclusion. Under the conditions of our experiments, obstruction of the proventriculus certainly occurred more readily in the case of fleas of the species *Xenopsylla cheopis* than with those of *Ceratophyllus fasciatus*."

Otten, while carrying out transmission experiments with *Pygiopsylla ahalae* in Java, observed a peculiarly protracted course of the disease in guinea-pigs having an average duration of 16 days before death. This flea appears to play only a small part in the spread of plague in Java, owing to its preference for outdoor breeding places, but may turn out to be a less efficient carrier than *X. cheopis*, which is acknowledged to be the principal plague flea of Java.

McCoy (1921) showed that *Ceratophyllus acutus* could transmit plague between ground squirrels but the disease in nature tends to assume a subacute or chronic form.

Gauthier and Raybaud (1903) were the first to definitely prove that plague was transmitted by fleas. It would appear from the results of their flea survey of Marseilles, where the experiments took place, that nearly all the fleas used must have been *X. cheopis*.

FACTORS GOVERNING THE DISTRIBUTION OF RAT FLEAS.

The studies in the geographical distribution of the species of the animal kingdom by Darwin and Wallace showed, that isolation over long periods of geological time was the important factor determining the evolution of characteristic species in a particular locality. History affords many instances of the disastrous effects following an abrupt alteration in the balance of nature by the introduction of a new species of animal or animal parasites into new areas, as the result of the opening up of new means of communication. The introduction of rabbits into Australia, of the *Anopheles* mosquito into Mauritius, and of the rat flea, *X. cheopis*, into Colombo are good examples.

The plains of Madras are largely isolated from the rest of India by mountain chains, while there is comparatively little short-distance commerce between the seaboard and *X. cheopis* infested zones.

X. cheopis is already found in some parts of the plains of the Madras Presidency. I believe that unless due precautions are taken this flea will eventually become established along the whole seaboard of Madras.

I will now endeavour to show that the *factor of importation of a foreign flea* is responsible for the spread of plague in Colombo and several other cities, and that the distribution of *X. cheopis* and *X. astia* in Colombo shows wide variations within a restricted area under the same climatic conditions, and that the prevalence of *cheopis* is closely correlated with that of human and rat plague.

XENOPSYLLA CHEOPIS AND IMPORTED PLAGUE.

Plague was first introduced into Colombo late in December, 1913, in cargoes of rice from Nagapatam, a South Indian seaport within short range of Colombo, then suffering from its first plague epidemic. The disease broke out in the centre of the grain trade in a street near the harbour, mainly composed at that time of privately owned rat-infested godowns, but now mainly devoted to the trade in piece goods. As we have seen, *astia* alone was found upon the rats of Colombo prior to the outbreak of plague; shortly afterwards (January, 1914) *cheopis* was discovered for the first time on the rats of Sea Street near the spot where plague broke out.

The bulk of the rice is now stored in Government granaries specially designed to reduce rat infestation. Other kinds of grain are distributed from rat-free municipal shops and private godowns in the Pettah District, many of which are considerably improved. Various markets form subsidiary centres for grain distribution.

The proportion of *X. cheopis* to total rat fleas in the Government granaries and customs premises is over 70 per cent., in the Pettah godowns about 25 per cent., in the retail markets 6 to 8 per cent., in the rest of the town less than 1 per cent., the remaining fleas being *X. astia*.

Moreover, if *X. cheopis* does happen to be found in an outlying district, it is usually easy to trace its origin to recent imports of grain or fodder from the Pettah or Slave Island stores, where *X. cheopis* abounds. The relation of the distribution of both human and rat plague to the storage of imported grain and other forms of merchandise is just as striking. Plague is endemic in Colombo in the vicinity of the large godowns for imported merchandise, and of the markets mentioned. The disease is also endemic in certain streets, including Sea Street, connected to the Pettah zone by a system of underground untrapped drains. Elsewhere plague only occurs sporadically.

It is only of recent years that the importance of the grain trade in relation to the spread of plague has become fully realised. The Interim Report of the Advisory Committee for Plague Investigation in India contains no reference to the subject. Norman White, however, while Sanitary Commissioner for the Government of India, in a paragraph of his report on "Twenty Years of Plague in India," quoting fresh illustrations of "the excessively great importance of the movements of grain and other merchandise in the transference of plague infection from place to place," refers to the grain trade in plague-infected India as in a very special sense a dangerous trade.

Glen Liston, at the conclusion of his Milroy Lectures, stressing the urgent need of international control of sea-borne commerce from plague-infected ports, shows how the danger can be dealt with by fumigation of the suspected merchandise with hydrocyanic gas by methods largely developed by himself.

Turning again to India we find that in Madras the population of those parts of the Presidency which are relatively free from plague subsist on locally-grown rice. If grain, owing to exceptional circumstances, is imported in bulk from plague centres to these parts severe epidemics have been known to follow. Thus imports of grain into Vizagapatam in 1917 were in marked excess of any previous year and plague broke out for the first time. Turning to Cragg's papers we find that the rat fleas of Vizagapatam were 48·2 per cent. *cheopis* in 1920.

In the United Provinces, Banda was free from plague. Here also Glen Liston attributes this freedom to the climate.

In the Tenth Report of the Plague Commission we read as follows: "the climate [of Banda] would appear to be not very different from Cawnpore, so that the absence of severe epidemic plague cannot be attributed to the influence of climate."

The plague-ridden city of Cawnpore has been described as one large granary.

I have no information regarding the species of flea prevailing on the rats of these two towns, but I venture to predict, that if the conditions are as formerly, then *X. cheopis* will be found to be prevalent on the rats of Cawnpore godowns used for the storage of imported grains, and *X. astia* on the rats of Banda, where the inhabitants subsist on locally grown produce.

Measures devised for the protection of grain from rat depredations fulfil the double object of reducing the number of both rats and fleas, since fleas cannot multiply indefinitely without rat blood.

If my theory is accepted that the danger of transferring plague in grain largely depends on the particular species of flea prevalent on the rats in the grain stores, then special importance attaches to the disinfestation of grain in transport from centres where the more efficient plague-carrying fleas are found.

The danger is two-fold.

A focus of actual infection may be set up by the transference from place to place of infected *cheopis*; or a focus of potential infection by the establishment of *cheopis* on the rats of a locality where the flea was not formerly indigenous.

Most epidemiologists associate the special danger of the grain trade with the rapid multiplication of rats promoted by access to a favourite and abundant food.

The rat population factor is undoubtedly important, but it is offset by the increased immunity of the rats to plague infection which develops wherever plague is prevalent.

If this be the only factor involved, how is it possible to explain the fact that the storage of *Ceratophyllus* and *X. astia* infested grain does not appear to be particularly dangerous? The immense traffic in grain from *Ceratophyllus* infested ports does not seem to give rise to plague.

Prior to the outbreak of plague in Colombo when *astia* alone was present, no special precautions were taken to safeguard the granaries from the rats which swarmed in such numbers in them all. Yet there was no plague. Since the disease appeared, vast improvements have been made. The bulk of the grain is stored in warehouses designed to be rat free, special regulations are in force for the control of the grain trade. Yet plague has several times been transported in *cheopis* infested grain to parts of the island never before infected in the history of Ceylon.

It may be asked how is it possible for the spread of a particular species of flea to be associated with merchandise?

The explanation lies in the bionomics of the various species.

For example, as Bacot pointed out, larvae of *C. fasciatus* cannot develop without feeding on the faeces of the adult flea.

In practice this means that the flea can only multiply in association with

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the rat nest. In granaries, ships' holds and warehouses, the produce is constantly being shifted so that the rats have difficulty in establishing a fixed habitation.

The larva of *X. cheopis* on the other hand can be readily reared on grain debris alone and can develop to maturity almost anywhere.

The eggs of the flea stick to the gunny bags. Everything favours the transference of this particular flea.

In Marseilles, Japan and Australia it has been shown that *X. cheopis* is much more prevalent on the seaboard than in the interior.

In all three regions the seasonal incidence of *cheopis* varies, the period of maximum prevalence corresponding in each case to the season when plague is liable to occur.

Kitasato has recorded his belief that though Ceratophylli are the most prevalent fleas in Japan, plague is mainly spread by *X. cheopis* imported from India. Ferguson reports that *X. cheopis* is only found on introduced rats in New South Wales, and is of opinion that *X. cheopis* is the species primarily responsible for the spread of plague from rat to man in Sydney.

Ham (1907) in his report on plague in Queensland writes "it is unnecessary to point out that the distribution of *Pulex cheopis* both in time and place, has its strange counter part in that of epidemic and, perhaps, also epizootic plague."

It is noteworthy that the miscellaneous species of flea found on the tarabagan of Manchuria, the wild rodents of the South African veldt, the rabbits and hares of Suffolk, the squirrels of California, are all apt to be associated with smouldering enzootics of plague among the rodents themselves, and outbreaks of pneumonic plague among human beings.

Wherever *X. cheopis* prevails in a suitable climate the rats are liable to acute epizootics and human beings to epidemic bubonic plague with comparatively few cases of pneumonic plague.

Distribution of *X. cheopis* and *X. astia* in relation to Plague in Colombo.

On resuming my observations on plague in Colombo in 1920–21 after my return from war service, I discovered that the distribution of *X. cheopis* on all species of rats was remarkably irregular, and corresponded closely with that of human and rat plague. The results obtained from a collection of fleas made in the plague and non-plague areas respectively, and part of the result of a more comprehensive survey, have already been reported (1923). For the purpose of this rat flea survey of Colombo, the area comprised within the city limits has been divided into 15 districts, having as far as possible natural boundaries, such as lakes, rivers, bunds and canals. Zones surrounding the principal markets, customs and grain granaries have been marked off by artificial boundaries.

The fleas found on the rats throughout each district have been systematically collected during the two plague seasons 1922–23 and 1923–24. Full details will be reported elsewhere, but as the main results have an important bearing on my argument they will be summarised below.

Table I.

District	No. of premises	No. of rats searched for fleas	No. of fleas	No. of *cheopis*	Percentage *cheopis*	Plague incidence per 10,000 of population. 1920–1924	Plague incidence per 10,000 of population. Actual period of survey
A	117	270	965	276	28·6	128·9	63·1
B	119	293	939	131	13·95	83·6	22·05
C	85	239	798	46	5·76	45·2	20·8
D	95	255	846	49	5·79	45·9	12·9
E	123	284	985	8	0·81	23·6	4·4
F	138	334	883	16	1·81	12·2	2·8
G	297	663	1821	29	1·59	7·5	2·5
H	65	151	502	7	1·39	13·6	5·9
I	57	113	375	Nil	Nil	2·9	3·7
J	77	175	463	4	0·86	0·9	Nil
K	59	102	328	2	0·6	0·9	Nil
L	65	146	469	40	8·53	47·6	10·8
M	23	75	200	14	7·0	53·1	19·3
N	34	67	348	16	4·59	7·4	Nil

The figures in the above schedule apply only to *Rattus rattus*. A much smaller collection of fleas was made on *R. norvegicus* with a similar general result.

The prevalence of *cheopis* in the principal plague zones was remarkably similar during the two plague seasons, 1922–23 and 1923–24, being 29·78 and 28·09 for area A, The Pettah; 15·46 and 13·23 for area B, Sea Street; 4·27 and 4·74 for area D, Slave Island; 8·05 and 8·75 for area L, Deans Road Market.

Table II.

District	Acreage	Population	No. of rats caught 1922	No. of rats caught per 100 traps laid	Flea-index	Percentage *norvegicus* of total rats
A	129	7,601	4,040	14·52	2·83	32·55
B	124	19,954	6,045	15·36	2·89	18·75
C	120	11,492	5,207	18·61	2·26	21·63
D	331	21,564	9,918	22·83	2·37	5·00
E	222	24,478	7,052	16·61	2·43	22·08
F	1592	45,571	19,380	22·88	2·08	8·13
G	2909	39,568	19,437	18·3	1·86	12·00
H	300	11,762	4,512	19·48	1·47	11·30
I	470	13,355	5,806	14·96	2·2	25·76
J	891	21,288	10,552	21·76	1·8	2·19
K	620	10,813	5,983	18·67	2·53	1·5
L	181	11,957	7,192	18·95	1·96	10·45
M	53	2,070	975	23·3	2·54	—
N	237	2,690	—	—	—	36·2

The human population figures are taken from the census of 1921. The wide fluctuations in commercial prosperity during the period 1921–24 resulted in a considerable ebb and flow of population. The incidence of plague on the various districts during 1921 itself, however, was similar to that shown above. The human plague records are probably more accurate than those of any other eastern city.

Table III.

	Madras City		Colombo		Bombay		Banda		Cawnpore	
	Mean monthly temp.	Saturation deficiency	Mean monthly temp.	Saturation deficiency	Mean monthly temp.	Saturation deficiency	Mean monthly temp.	Saturation deficiency	Mean monthly temp.	Saturation deficiency
January	75·1	·23	79·1	·22	73·0	·23	61·6	·11	61·5	·08
February	76·7	·24	80·2	·24	74·8	·23	68·5	·16	67·3	·18
March	80·0	·26	82·1	·26	74·8	·29	75·3	·42	74·3	·48
April	84·0	·30	82·5	·25	82·2	·28	86·2	·64	82·5	·63
May	86·7	·41	82·4	·20	86·2	·34	95·4	·91	88·9	·80
June	86·4	·47	81·0	·20	83·8	·20	97·6	·84	89·8	·62
July	84·5	·41	80·6	·19	80·2	·12	86·1	·18	84·1	·21
August	83·3	·34	80·8	·18	80·8	·15	83·9	·11	82·6	·15
September	83·0	·31	80·8	·22	79·5	·14	82·8	·20	80·5	·23
October	80·6	·22	80·2	·19	80·6	·20	81·4	·45	74·8	·27
November	77·5	·19	79·9	·19	79·5	·30	63·7	·07	67·3	·16
December	75·5	·20	79·2	·21	76·1	·21	59·9	·06	59·9	·10

The method of estimating rat population by number caught per 100 traps laid, though the best available, is open to various fallacies.

It may be argued that the relatively low rat population shown in these figures for the principal plague areas may be attributed to the amount of grain and other food-stuffs available for the rats in the vicinity of the traps. This, however, cannot apply to area B, where the percentage of *cheopis* and the incidence of rat and human plague remain high though the grain has been removed.

The district is in communication with area A, through a series of large untrapped underground drains dating back to the Dutch occupation.

Moreover, the rat infestation of the larger stores must have been considerably reduced by structural improvements.

The flea-index is calculated on a total of 2280 fleas taken off rats brought to the laboratory in flea-proof bags containing *Rattus rattus* only. It will be noted that relatively more fleas are caught in the populous districts, which is in accordance with the observations of Steenis in Java.

The coefficient of correlation between both periods of human plague incidence, and percentage *cheopis* to total rat fleas in the first 14 districts is ·95 probable error ± ·02; this is a highly significant figure, much higher than might be expected considering the multiplicity of factors affecting the result.

I am much indebted to Mr C. A. Pate, Officer in charge of Rat Destruction, for the figures of rats trapped, and to Mr L. J. B. Turner, Director of Statistics, Ceylon, for re-distributing the population of Colombo into the new districts and for calculating the coefficient of correlation.

The distribution of endemic plague in Colombo is altogether different to that of enteric fever and does not correspond to the zones of excessive infantile mortality.

The relation of the rat epizootic to *cheopis* infestation in Colombo can be shown on a spot map. The correspondence is most remarkable between the distribution of premises where plague-infected rats were found in the course of ordinary routine work of the Public Health Department and the location of *cheopis*-infected rats examined for the systematic flea survey. The customs' premises and 4th Cross Street, the localities where rat plague is most prevalent, are precisely those showing the highest *cheopis* infestation.

The percentage of *cheopis* varied from 30·5 during the months of November, 1923, to a minimum of 9·8 in May, 1923, on the rats of the endemic zone in Colombo.

These figures, being influenced by importation, do not represent the true seasonal carry over of *cheopis* in this locality.

The extent of this carry over considerably affects the prospect of eradicating the disease completely. It is noteworthy that a spell of relatively dry years followed the outbreak of plague in Rangoon (1905), which probably helped to delay considerably the establishment of plague and *cheopis* in Colombo. Rangoon was the ultimate source of the infection in the case of both Negapatam and Colombo.

SUMMARY AND CONCLUSIONS.

The geographical distribution of the different species of rat flea is one of the most important factors governing the spread of plague.

Xenopsylla cheopis is the most effective transmitter of both epidemic and epizootic bubonic plague in all parts of the world.

The relative immunity of certain parts of India and Ceylon from plague is to be primarily attributed to the prevalence of an inefficient plague-carrying flea on the rats of these localities, viz. *Xenopsylla astia*.

Climatic conditions play only a secondary part in limiting the spread of the disease in these relatively plague-free localities.

Plague infection can be maintained in such localities by the importation of *cheopis*-infested merchandise.

Climate does not exert an equal effect upon the transmitting power of different species of flea.

Numerous attempts to transmit plague from rat to rat by means of *X. astia* at room temperature during the plague season in Colombo have all failed. *X. astia*, however, can carry plague from rat to rat under climatic conditions favourable to plague transmission. Continuous transmission of plague from rat to rat has been obtained with *X. cheopis* in Colombo under exceptionally unfavourable climatic conditions.

Both plague and *X. cheopis* have a very irregular distribution within limits of Colombo City. The coefficient of correlation between two periods of human plague incidence and percentage of *cheopis* to total rat fleas of all species in 14 districts of the city is ·95, probable error $\pm$ ·02 for both periods.

There is a close relation between premises infested with *X. cheopis* and premises where plague-infected rats are found.

A three-fold relationship exists between the amount of imported grain, the prevalence of *cheopis* on rats, and the incidence of plague in the localities where grain is stored in Colombo.

The measures so far devised for combating plague among Oriental populations, tolerant of all forms of animal life, have not proved conspicuously successful.

Due recognition of the importance of the flea species factor should lead to marked improvement in plague preventive measures in many parts of the world.

A rat flea survey of all the principal plague areas, especially the ports, becomes urgently necessary.

The exports from localities where *X. cheopis* is found to be prevalent upon the rats should be considered actively dangerous when the locality is plague infected, and potentially dangerous even if it is plague free, since the continual importation of *cheopis* into a locality where this flea is not indigenous may eventually result in the extension of plague infection to a new area.

I agree with Glen Liston and Norman White, that the export of produce, especially grain, from plague-infected ports should be controlled by international agreement.

The limitation of imported *cheopis* and plague to definite zones in such localities as Colombo greatly facilitates the task of plague prevention, since all available resources can be concentrated simultaneously, or successively, on the infected areas.

In such instances it is possible to mark out the potentially plague-infected zones by the simple and accurate method of surveying the rat fleas.

Ten years have now elapsed since I tentatively put forward the suggestion that the spread of epizootic plague in the East Indies might be governed by the flea species factor. At first I adopted a cautious attitude towards my own hypothesis. I believe that the evidence now available warrants its acceptance by epidemiologists without further hesitation.

If so, the discovery is but further testimony to the essential unity of science in its bearings on the welfare of the human race, for it is the natural outcome of the purely zoological researches of Rothschild and Jordan on the systemics of the Siphonaptera.

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