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Rats cannot have been intermediate hosts for *Yersinia pestis* during medieval plague epidemics in Northern Europe

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ABSTRACT

The commonly accepted understanding of modern human plague epidemics has been that plague is a disease of rodents that is transmitted to humans from black rats, with rat fleas as vectors. Historians have assumed that this transmission model is also valid for the Black Death and later medieval plague epidemics in Europe. Here we examine information on the geographical distribution and population density of the black rat *(Rattus rattus)* in Norway and other Nordic countries in medieval times. The study is based on older zoological literature and on bone samples from archaeological excavations. Only a few of the archaeological finds from medieval harbour towns in Norway contain rat bones. There are no finds of black rats from the many archaeological excavations in rural areas or from the inland town of Hamar. These results show that it is extremely unlikely that rats accounted for the spread of plague to rural areas in Norway. Archaeological evidence from other Nordic countries indicates that rats were uncommon there too, and were therefore unlikely to be responsible for the dissemination of human plague. We hypothesize that the mode of transmission during the historical plague epidemics was from human to human via an insect ectoparasite vector.

1. Introduction

Since 1998, a number of studies of ancient DNA and of immunoproteins from presumed plague victims have conclusively shown that many of the different historical epidemics that were called 'pestis', 'plague' and the like, and which killed a high percentage of the populations of European countries between the mid-fourteenth century (the Black Death) and the mid-seventeenth century, were caused by *Yersinia pestis*. Thus, the disease involved was the same as modern plague (Drancourt et al., 1998; Raoult et al., 2000; Bianucci et al., 2009; Haensch et al., 2010; Tran et al., 2011; Kacki et al., 2011; Bos et al., 2011; Bianucci et al., 2007). *Y. pestis* DNA sequences have also been detected in skeletons buried in the second half of the sixth century (Wiechmann and Grupe, 2005; Drancourt et al., 2004, 2007), indicating that the first known plague pandemic, the 'Plague of Justinian', was also caused by *Y. pestis*.

These results definitively refute the hypothesis put forward by the microbiologist Shrewsbury (1970), the zoologist Twigg (1984), the demographer Scott and the physiologist Duncan (2001), and the historian Cohn (2002), that some or all of the medieval plagues in Europe must have been different diseases in medical and bacteriological terms from modern plague. However, even though their main hypothesis has been refuted, some of their arguments are still valid and show that we need to reconsider our understanding of how historical plague epidemics in Europe were disseminated.

Modern plague reached Hong Kong in 1894 from other parts of China, and spread first to India and later to all inhabited continents. Alexandre Yersin showed that the disease in Hong Kong was caused by a bacterium, later named *Y. pestis* (Yersin, 1894). It was also Yersin who claimed that he had found the cause not only of plague in China, but also of the medieval and early modern plague epidemics. Four years after the discovery of the bacillus, Paul-Louis Simond proposed the transmission route from the black rat (*Rattus rattus*) via the rat flea (*Xenopsylla cheopis*) to humans (Simond, 1898). The scientific community was not fully convinced until ten years later, since this hypothesis did not explain all observations (Report of the Indian Plague Commission, 1901; Low, 1901; Hope, 1902; Hankin, 1905; Colvin, 1908; Martin, 1911; Bacot and Martin, 1914). However, the weaknesses of the hypothesis were soon forgotten, which is easily understood when we remember that the doctors and epidemiologists who were working in India and other countries at that time were facing a worsening and very serious

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epidemic. Within a few years, the accepted medical understanding of plague epidemics was that they started with epizootics among rodents transmitted by fleas, mainly *X. cheopis*. From various other rodent species, *Yersinia* was transmitted to black rats which lived close to humans. When most of the rats in an area were dead and cold, the rat fleas searched for new hosts outside the rat population and thus infected humans (Bacot, 1915). Different aspects of the rat → rat flea → human transmission mechanisms were investigated in detail during the early part of the twentieth century, and although it was acknowledged that other flea species could sometimes transmit plague, it was generally claimed that only the transmission route from rats to humans via the rat flea was efficient enough to sustain a major epidemic of human plague (Burroughs, 1947; King and Pandit, 1931; Tiraboschi, 1904). This transmission route would result in an epidemic that spread slowly, only 12–15 km/year, as observed in some areas of India in the 1890s (Report of the Indian Plague Commission, 1901; Liston, 1924). Humans could carry the infection to new areas ('metastatic spread') by transporting sick rats or infected fleas, but humans in the new area would not be infected until the rat population in the new area had been infected and most rats had died (Hankin, 1905). Only then did the rat fleas approach humans. This was shown to take approximately three or four weeks (Martin, 1911). An important element of this transmission hypothesis was that infected humans could not transmit the disease to new areas. In the 1920s and 30s, this interpretation of plague epidemics was disseminated to the medical world by plague manuals for medical and public health workers published by the League of Nations Health Organization (Wu et al., 1936). The English bacteriologist Fabian Hirst, who had worked with plague in the microbiological laboratory in Colombo on Ceylon from 1912 to 1934, published an important monograph, *The conquest of plague* (Hirst, 1953). This has clearly been important for historians, since it is usually quoted in historical works on plague epidemics, even in discussions of topics where Hirst has been shown to be mistaken (Meyer, 1942, 1954).

Yersin believed he had found the causative agent not only for the epidemic in Hong Kong in 1894, but also for the Black Death and subsequent plague epidemics in Europe in medieval and early modern times (Yersin, 1894). This view was soon accepted by historians (Abel, 1900). However, many of them ignored the obvious differences between descriptions of ancient and modern plague epidemics in the written sources. Cohn wrote: "Without argument, historians and scientists have taken the epidemiology of the modern plague and imposed it on the past, ignoring, denying, even changing contemporary testimony, both narrative and quantitative, when it conflicts with notions of how modern bubonic plague should behave." (Cohn, 2002). Cohn and like-minded scholars put forward two main arguments against using the rat-flea model from India to explain the spread of plague in medieval and early modern Europe:

1. There is a complete lack of evidence of any involvement of rats and rat fleas in the historical epidemics.
2. The speed of transmission of the epidemics was very different. Medieval epidemics spread extremely rapidly, modern epidemics rather slowly.

Cohn and like-minded scholars also claimed that the signs and symptoms described for modern and medieval plague were different. However, one of the present authors (LW) has previously concluded that on the contrary, the limited number of historical documents containing detailed descriptions of the clinical disease give a clinical picture very similar to descriptions of untreated modern bubonic plague and sometimes untreated pneumonic plague (Walloe, 2008). But the two arguments above remain valid. The 'revisionists' from Shrewsbury to Cohn originally used these two difficulties to argue that medieval plague must have been another disease than modern plague. This conclusion is no longer tenable, and we must try to find another explanation (Little, 2011). This is the purpose of the present paper.

1.1. Biology of rats and transmission of plague

Shrewsbury claimed that the medieval rat population was only large enough to maintain a plague epidemic in the major towns of Britain and not at all in the countryside (Shrewsbury, 1970). This argument was later strengthened by the zoologists Twigg (1984) and Davis (1986), who claimed that black rats were evolutionarily adapted to a tropical and subtropical climate (South China and India and areas between) (Gillespie, 2004; Becker, 1978a), and that they could not reproduce effectively in the British Isles. Davis had spent his whole professional life working on populations of black and brown rats in the cities and countryside of the US. He judged that populations of black rats in northern European countries could not be sustained without a continuous supply of new individuals (from ships). He wrote: "Application of this information/on the biology of black rats/to rat populations of the Middle Ages produces the following scenario: *R. rattus* may have persisted in towns, especially grain ports, but the number of buildings with rats was small and the number of rats was stationary. The population in a particular town disappeared in a few years, but might again become established as a result of new introduction. These characteristics held for northern France, Scandinavia, and the British Isles, but in the more southern Mediterranean region of France *R. rattus* may have lived in small numbers in rural areas." (Davis, 1986). Davis' conclusion was that *R. rattus* was rare or absent in most of Europe in medieval times and in the early modern period.

However, there is no doubt that rats were important intermediate hosts during historical plague epidemics in warmer countries, as they were in China and India at the beginning of the twentieth century (Report of the Indian Plague Commission, 1901; Martin, 1911; Baber, 1878; Lowry, 1882). The records often include dramatic descriptions of rats appearing from their hiding places, vomiting blood, and dying. The plague expert Wu Lien-Teh quoted a Chinese poem from 1792: "Few days following the death of rats men pass away like falling walls." (Wu et al., 1936). Records from warmer countries describe diseased rats everywhere, sick rats falling from roof-beams and dying rats piled in the streets, whereas northern European sources include no references to rats. The absence of any mention of rats, for instance during the plague epidemics in London in the 1600s, has traditionally been explained by assuming that rats swarmed everywhere at the time, so that there was no reason to write about them. However, healthy rats are seldom seen, whereas rats suffering from plague behave quite differently. Pepys, who described trifling observations and events in great detail, makes no mention of sick or dead rats, nor does Absalon Pederssøn in his diary, which contains detailed descriptions of a plague epidemic in Bergen, Norway, in 1565–66 (Pederssøn, 1860). Another, and in our view more likely, explanation for the complete lack of references to rats in European plague epidemics, is that there were very few rats in northern Europe at the time, as claimed by Shrewsbury, Twigg and Davis.

Shrewsbury and Twigg's argument that the climate was too cold for black rats in England would of course apply even more strongly to Norway and the other Nordic countries. Written records provide information on about 26 plague epidemics in Norway and Sweden between 1349 and 1654, or one every 12 years on average, most of them affecting a large part of the Scandinavian Peninsula, and some spreading as far north as the Lofoten Islands (Walløe, 1995). Some of these epidemics are described in detail and some are in direct continuation with plague epidemics in other countries. Plague has specific symptoms which are easy to recognize during an epidemic when many people are affected, and which are quite different from symptoms of other communicable diseases. It is therefore reasonable to assume that during this period, the term 'plague' ('pest' in Norwegian and Swedish) was used for this disease only. Since the recent findings from studies of bacterial DNA and immunoproteins from plague victims in other European countries make it most reasonable to assume that the Scandinavian epidemics were also caused by *Y. pestis*, it is particularly important to compile all available information on the distribution of black rats in the Nordic countries from this period.

1.2. Historical information on rats on the Scandinavian Peninsula

Today the brown rat (*Rattus norvegicus*) is the most common rat species in Europe (and North America), and most people's knowledge of rats relates to this species (Armitage, 2004; Telle, 1966). Even though black and brown rats are very similar in appearance, their biology and behaviour are quite different (Eibl-Eibesfeldt, 1952; Ewer, 1971). The brown rat originates from the northern parts of China and Mongolia. From here, it moved southwards and westwards with people. Zoologists and archaeologists agree that the brown rat first reached Europe from Russia in the eighteenth century, and that it did not spread to all European countries until about 1800. One important difference between black and brown rats is that the brown can tolerate much lower environmental temperatures than the black (Herter, 1950). The brown rat digs and swims, whereas the black rat climbs and dislikes water (Benick, 1924). Until about 1950, the rats found climbing around ships were always black rats (Matheson, 1939; Bentley, 1959). The two species have very similar skeletal morphology. Skeletons can in general only be distinguished by the shape of the skull, and, in young individuals, by the teeth (Becker, 1978a,b).

The zoologists Lilljeborg and Collett, who in the nineteenth century systematically studied the distribution of mammalian species in Sweden and Norway, found only a few populations of the two rat species, mainly in towns (Lilljeborg, 1874; Collett, 1876, 1883). According to Collett (1876), both species "are still absent in all the more remote valleys, in both the mountains and the upper parts of the main valleys, for example Valdres and Gudbrandsdalen; and they are also absent or only found in small numbers in several coastal regions, especially on the islands." Lilljeborg and Collett also quoted earlier authors who conveyed the same information. According to these sources, the distribution of both species of rats on the Scandinavian Peninsula had been limited and very patchy for a long time up to the 1870s. However, when considering descriptions by earlier zoologists it should be remembered that we know very little about the methods they used, and thus how accurate their findings were. Thus the most reliable source of information about the history of vertebrates in Norway and Sweden – and in many cases the only source – is skeletal material found in the soil at ancient settlement sites in caves or under rock shelters. Most such finds are made during archaeological excavations.

2. Archaeological evidence of black rats in Norway

Animal bone assemblages found during archaeological excavations in Norway are kept in the Natural History Collections at the University Museum of Bergen under the supervision of one of the present authors (AKH). The museum now has collections of bone assemblages from more than 1600 sites. Most of the finds are small, but certain of them contain tens of thousands of bones from various species, including fish, birds and mammals. Fig. 1 shows a map of the archaeological locations mentioned in the text. The largest medieval collections are from the towns of Hamar, Oslo, Tønsberg, Stavanger, Bergen and Trondheim, from trading centres in the Sogn and Møre districts of Western Norway, and from farm middens in Nordland and Troms counties. For example, almost 25 000 bones belonging to about 70 different vertebrate species have been identified in12 medieval bone assemblages from Tønsberg. They include small species such as frogs, toads, herring, eels, magpies and red squirrels. A total of 221 rat bones have been identified in six of the 12 assemblages. All the archaeological projects carried out in Norway have produced a total of 702 rat bones in 19 assemblages from 19 different localities. Table 1 contains information about all the rat bone assemblages which have been found in Norway. Some of this information has previously been published in Norwegian (Hufthammer and Walløe, 2010). All are from the Middle Ages or soon after the Lutheran Reformation (AD 1536-37). The oldest rat bone from Norway has been radiocarbon-dated to 755 $\pm$ 70 BP (TUa 804), calibrated age range AD 1225-95, and is a pelvic bone that was found at Bryggen, the Hanseatic wharf area of Bergen. Altogether, 31 of the bones (skulls, mandibles and teeth) have been identified as black rat. It is highly likely that the 671 bones that have only been identified as rat (*Rattus* sp) are also from black rats. Most of these are limb bones, vertebrae and pelvic bones, which lack reliable diagnostic features for identification to species. In several cases, assemblages of bones have been found, probably representing the remains of several individuals. One such assemblage was found in Tønsberg, at Storgaten 24–26. It consisted of 206 rat bones, all from

Fig. 1. Map of archaeological locations mentioned in the text. The sites shown in North Norway (Nordland, Troms and Finnmark counties) are a selection of those with significant numbers (>2000) of identified animal bones. Bone assemblages from medieval Norwegian towns include those from coastal towns containing rat bones (see Table 1) and 86 other assemblages containing large numbers of identified animal bones (Table 2). There are no rat bones in any of the assemblages in the latter category.

Table 1
The table indicates which Norwegian medieval finds contain rat bones (museum catalogue number and site), town and site, the total number of rat bones with the number of bones identified as black rat in brackets, the dates of the site and the references that have been used. As discussed in the text, it is highly likely that all the rat bones from this period are of black rat. University Museum means the University Museum of Bergen, NIKU is the Norwegian Institute for Cultural Heritage Research and Riksantikvaren is the Directorate for Cultural Heritage.

Museum number (JS)	Locality	Total number of rat bones	Age	References
577	Oslo, Gamlebyen, søndre felt	9 (3)	AD 1100–1250	Schia 1987, Archive, University Museum.
628	Oslo, Kontraskjæret	68	AD 1624–1730	Archive, University Museum.
768	Oslo, Kanslergaten 10	20	AD 1200–1350	Lie, 1991.
702, 809	Oslo, Nordre felt I and II	323 (12)	c. AD 1050–1500	Pers. comm. P. Molaug, NIKU. Archive, University Museum.
1322	Oslo, Bygdøy kongsgård	1	13th–16th Century	Karlberg andSimonsen, 2008, p.36. Archive, University Museum.
1530	Oslo, Arupsgate	1	Medieval	Archive, University Museum.
563	Tønsberg, Storgaten 35	1 (1)	12th–17th century	Pers. comm. Jan Eriksson, Riksantikvaren. Archive, University Museum.
637	Tønsberg, Storgaten 24/26	206 (11)	12th –16th century (Tua805:715 ± 70 BP)	Archive, University Museum.
644	Tønsberg, Baglergaten 3	6 (1)	c. AD 1200–1350	Brendalsmo, 1983. Archive, University Museum.
664	Tønsberg, Baglergaten 2-4	2	AD 1200–1350	Pers. comm. Jan Brendalsmo, NIKU. Archive, University Museum.
694	Tønsberg, Øvre Langegate 57/59	4	c.14th century – recent	Flodin et al., 1983. Archive, University Museum.
763	Tønsberg, Storgaten33/Tjømegate	2	Medieval	Archive, University Museum.
519	Stavanger, Skagen 3	2	AD 1100–1272	Lillehammer, 1971. Archive, University Museum.
1398	Stavanger, Stavanger torg	15	Mainly more recent than 1550	Archive, University Museum.
397	Bergen, Bryggen	2	Medieval (Tua804: 755 ± 70 BP)	Archive, University Museum.
540	Bergen, Bryggen	1 (1)	c. AD 1100–1350	Archive, University Museum.
632	Trondheim, Televerkstomten	23 (2)	AD 900–1350 and AD 1580 and more recent	Marthinussen, K.L. University of Bergen.
765	Trondheim, Folkebibliotekstomten	2	AD 900–1125 and AD 1225–1475	Lie, 1989.
845	Trondheim, Erkebispegården	14	Mainly AD1537–1660	Hufthammer, 1999. Archive, University Museum.

one unit, which is a layer of waste below a building. Closer investigation showed that it contains bones from rats of all ages – very young, adult and old. It therefore seems highly probable that the bones are from the remains of a rat nest. A few of these bones, with a total weight of 60 mg, have been 14C-dated to the High Middle Ages; 715 ± 70 BP (TUa 805), with a calibrated age range of AD 1265–1375. Several assemblages of bones from rats of different ages have also been found in an area of medieval Oslo called “Nordre felt”, but not in the same quantities as in Tønsberg. These finds are evidence of breeding populations of black rats in Tønsberg and Oslo in the High Middle Ages.

In general, the Norwegian sub-fossil bone collection contains fewer finds from inland areas than from the coast, but inland finds include a variety of species, and in several cases appear to be representative of the local vertebrate fauna in the Iron Age and Middle Ages. For example, rich material from these periods has been found in the area east of Lake Mjøsa. At Åker farm, a few kilometres east of Hamar, several thousand bones were collected from waste layers from the Migration Period, and at least 60 species of birds, fish and mammals have been identified. They include 91 bones from small rodents belonging to six different species. Several bone collections dating from the Migration Period, the Late Iron Age and the Early Middle Ages have been found during excavations at the farm Valum in the same area. Studies have identified many bones of ground vole (*Arvicola terrestris*) and yellow-necked mouse (*Apodemus flavicollis*), but no rat bones. Large-scale excavations have also been carried out in and around the ruins of Hamar cathedral, but no rat bones have been found in the bone material collected. Small mammal species, including rodents, have been identified in this material, which probably dates from 1580 to 1850. Large-scale excavations at Tøftom and Vesle Hjerkinn in the Dovre region have also resulted in finds of bones, and a variety of small species have been identified. The farm Hjerkinn was an important coaching inn on the main north-south route between Trondheim and Oslo in the Middle Ages. It would be reasonable to expect anthropochorous species to spread along such routes, but no rat bones have been identified in these collections. Nor have any rat bones been found during the many excavations that have been carried out at medieval farming settlements in the northern counties of Nordland, Troms and Finnmark.

One of the few larger settlements from the Viking Age (800–1000) that has been excavated using only modern techniques is Kaupang in Vestfold county. This was probably Norway’s most important port and urban settlement in the Viking Age. Large-scale excavations were undertaken in 2000–03. To ensure that bone collections were representative, the material was passed through a 2 mm or 5 mm sieve. More than 2000 bones from the excavations have been identified to species, including small species such as herring and red squirrel, but no rat bones have been found (Barrett et al., 2007).

3. Discussion

It is generally difficult to make a good estimate of a species’ distribution and population density on the basis of bone finds. There are a number of possible sources of error and bias that must be assessed, for example collection methods, identification techniques and cultural factors (including building types in this case), and species biology. However, even with these reservations, we conclude that the pattern of the Norwegian finds of rat bones from coastal towns, with many bones in a few collections and none in most, indicates that black rats were patchily distributed (Tables 1 and 2). There are some 120 collections of bone material of varying size (51 of which contain more than 100 bones identified to species level) from the Middle Ages from the coastal towns of Oslo, Tønsberg, Stavanger, Bergen and Trondheim, but rat bones have only been found in 19 of these. It is also reasonable to conclude that there is nothing in the subfossil material to indicate that black rats ever occurred at high densities in any of these five coastal towns in Norway. The complete lack of rat bones in all finds from rural areas and from the inland town of Hamar indicates that black rats were confined to coastal towns, and that they spread to Norway from ships, as suggested by

Table 2
Overview of all sites included in this investigation. More than 100 bones have been identified to species/genus (NISP) level at all these locations. North Norway means the counties Nordland, Troms and Finnmark, and South Norway all other counties. High mountain sites are at an altitude of more than 900 m above sea level. All the sites in North Norway are coastal. Four of the rural sites in South Norway are lowland inland locations, and the remainder are coastal sites.

County	Urban sites	NISP	Rural sites	NISP	High mountain sites	NISP
Østfold			2	657		
Akershus			1	237		
Oslo	14	175,548				
Hedmark	4	2404				
Oppland			4	29,653		
Vestfold	12	23,413				
Buskerud					14	25,840
Telemark					2	1837
Aust-Agder						
Vest-Agder						
Rogaland	4	12,161				
Hordaland	13	30,481	2	266	7	28,767
Sogn og Fjordane			1	116		
Møre og Romsdal			10	37,599		
Sør-Trøndelag	4	82,577	4	1975		
Nord-Trøndelag			1	627		
Nordland			15	15,659		
Troms			15	66,227		
Finnmark			8	65,022		
Total						
Southern Norway	51	326,584	25	71,014	23	56,444
Northern Norway			38	146,908		

Davis. The present zooarchaeological data are inevitably patchy, but there is nevertheless reason to conclude that the archaeological finds give a reasonably accurate picture of the distribution of rats in settlements and towns in medieval Norway.

From Kaupang, there were trading routes southwards and southwestwards, one of them to Ribe in southwestern Jutland in Denmark. It is therefore interesting to note that there are no Late Iron Age finds of black rats from Ribe in Denmark or another Danish settlement that was part of Kaupang's trading network, Haithabu (Hedeby), now in Schleswig-Holstein, northern Germany (Aaris-Sørensen, 2009). On the other hand, 25 bones of black rat from the Early Middle Ages (c. AD 1050) have been identified from Haithabu (Reichstein, 1991). Only sixteen finds of rat have been made within Denmark's modern borders, the oldest being from 1260 and the most recent from the 1600s (Aaris-Sørensen, 2009), despite a large number of archaeological excavations where bones from many other small animals have been found.

The earliest documentation of the black rat in Scandinavia is from the east coast of Sweden, from the Viking Age town Birka. The oldest of the 39 rat bones that were found at Birka dates from the early ninth century (Wigh, 2001). Black rats have also been reported from the Viking Age settlements at Kättsta, a few miles north of the medieval town Uppsala (Gustafson et al., 2006). A number of bones of black rat from medieval and post-medieval times have been identified from the port of Nyköbing on the Swedish east coast. The oldest date from the late twelfth and the thirteenth century (Kraft, 2006). Black rat bones have also been found in the two oldest towns in present day Sweden, in eleventh century sediments in Lund near the southwestern coast (Bergquist, 1957) and in Sigtuna (Wigh, 2001). We cannot claim to have an exhaustive list of all Viking Age or medieval finds of rat bones from Denmark and Sweden, as we have for Norway, but the list above is likely to be fairly complete.

No rat bones have been reported from archaeological medieval excavations in Turku and Helsinki in Finland (Ukkonen, 2010). Furthermore there are no records of black rats from the Baltic countries. However, this may be partly because there are few osteological analyses and reports from Eastern European trading centres, and partly because of the collecting techniques used: samples have rarely been sieved through a fine mesh at digs in Estonia and Lithuania. However, material from an excavation in Tallinn, dated to the thirteenth and fourteenth centuries, has been sieved. Many small species were identified, but no rats (Lougas, 2010). The zooarchaeologists who have studied bone material from archaeological excavations in these countries all have a thorough knowledge of the history of the fauna of their countries. They have all concluded that if black rats were present in Finland or the Baltic countries during the Middle Ages, their distribution must have been limited and the population density low (Daugnora, 2010; Lougas, 2010; Ukkonen, 2010). Findings of subfossil remains of black rats are also extremely rare in northwestern Russia (Savinetsky and Krylovich, 2011).

The striking lack of black rat bones in the Norwegian archaeological material from rural districts and the inland town of Hamar, the sparse finds in material from the other medieval towns, must weigh heavily in the ongoing discussion on transmission mechanisms for medieval and early modern plague epidemics. It is likely that plague reached one or more of the medieval towns of Oslo, Tønsberg, Stavanger, Bergen and Trondheim by ship, carried by ships' rats, goods or infected people. Since rat population density was low, it is unlikely that black rats were a mammalian vector for plague epidemics in these towns, and it is inconceivable that they could have been responsible for the spread of plague epidemics in rural districts of Norway, either during the Black Death or during later epidemics.

In all the Nordic countries there have been large numbers of archaeological excavations at late Iron Age and medieval sites, which have produced a significant number of bone assemblages. However, rat bones have rarely been found. And when they are present, it is always in archaeological sites near the coast. Thus, the archaeological evidence suggests that the same conclusion can be drawn for Denmark, Sweden, Finland, northwestern Russia and the Baltic countries as for Norway: the black rat was rare, and its medieval distribution was patchy and restricted to areas near the coast or other trade routes. It is therefore not possible for black rats to have been responsible for the dissemination of epidemics of plague in these countries in medieval and early modern times.

We do not have sufficient information to judge whether archaeological evidence from the British Isles and continental Europe justifies a similar conclusion, but the reports we have seen, for example a lack of rat bones in barn owl pellets (O'Connor, 1982), definitely point in the same direction (Armitage, 1994).

3.1. Hypotheses about the transmission of human plague

All the 'revisionist' authors share one assumption, which explains most of their arguments, although the details differ. They take it for granted that Simond's infection model, black rat → rat flea → human, which was developed to explain the spread of plague in some areas of India, describes the only possible way for an epidemic of *Y. pestis* infection to spread. From Shrewsbury to Cohn, these authors have argued that the prevailing climate would have made it impossible for black rats and the *X. cheopis* flea to have lived in northern European towns and countryside in medieval times, at least in the numbers necessary to maintain an epidemic of plague. We agree with this, but not with the assumption that rats and *X. cheopis* fleas are necessary for a human plague epidemic to spread. Simond's model certainly explained to some extent what happened in India. But the main reason why his hypothesis was not accepted at once was that it did not explain all the observations. According to

Simond's hypothesis, the spread of infection from one village to the next should be slow, because the rat population has to become infected and die before rat fleas will seek humans as a source of blood to any great extent. This process takes at least three weeks, sometimes four (Martin, 1911). Such a delay was indeed observed and reported from districts where rats and rat fleas were the main mode of transmission. However, in 1901 the Indian Plague Commission also reported in great detail a number of cases where transmission was saltatory (one infected person travelled, and the epidemic spread immediately and rapidly from him at the new location), cases and districts where no rats, dead, sick or healthy, could be found even after thorough search, and cases where plague was transmitted by merchandise (mainly grain and clothes) (Report of the Indian Plague Commission, 1901). The bacteriologist Hankin, who worked at the government laboratory in Agra during this period, was quite clear in his conclusions in 1905 (Hankin, 1905): "Rats [are] not a necessary cause or agent in the spread of plague." And he gives many examples, two of which are: "In Garhwal out of forty outbreaks investigated by Planck, a rat mortality was only observed in eight", and "When the disease spread through the town [Hulbi], despite careful search, dead rats were never observed.'

The Indian Plague Commission also reported in great detail on an outbreak of plague in Scotland. In 1900, a ship carried plague to Glasgow. From the beginning of August to the end of September, 36 cases of plague (16 fatal) occurred in thirteen different houses near the docks, but far apart. The Commission wrote (Low, 1901): "The experience of Glasgow as regards the association of plague with rats is an exception to what has been the experience elsewhere, e.g. Bombay, Alexandria, Sydney, &c. For although rats were not unplentiful in the infected area, no sickness was observed among them either before, during, or after the outbreak in 1900. During the carrying out the plague preventive measures numbers of these rodents were caught in the infected locality, but in none of them could the bacteriologists, who specially made search, find any trace of the plague microbe. From the end of August to November, 236 rats were caught within the infected area, many of them in and about the infected houses, but as has been said no evidence of rat infection was discovered." It is surprising that the Plague Commission's report and the detailed report by Hankin published in a leading medical journal of the period have been ignored by historians, biologists and medical doctors interested in historical epidemics of plague.

Observations similar to those reported by the Plague Commission and Hankin have been made in many later modern epidemics, for example in Liverpool in 1901 and 1914 (Lethem, 1923) and in Turkey and Iraq in 1947–55 (Baltazard and Seydian, 1960). Thus, Simond's hypothesis could not explain how someone who was infected with bubonic plague through a flea bite could transport the disease to a different district. Nor could it explain why the disease was often confined to a particular household, infecting all its members, while neighbouring households were free of plague, since the territories of groups of rats, both black and brown, are known to be larger than a single urban house (Davis, 1953). However, there are well documented examples of saltatory transmission and confinement to households from many of the modern epidemics, and there are also apparently reliable descriptions from historical epidemics (von Knorre and Paasch, 1981).

Icelandic annals report that Iceland was ravaged by epidemics with high mortality in 1402–04 and 1494–95. The disease was called 'bráðasótt' or 'plága' and has traditionally been regarded as plague. Karlsson claims that Iceland was not colonized by rats until centuries later, and that these were therefore examples of epidemics of plague without rats (Karlsson, 1996). The argument is weakened somewhat by the fact that no symptoms except 'stinga' (sharp pain) and 'blóðspýju' (vomiting blood) are mentioned in the annals. These symptoms do not definitely show that the epidemics were plague.

If rats are not involved in a particular epidemic of plague, it is also unlikely that the rat flea *X. cheopis* is involved. Indeed, there are many examples of modern epidemics where no *X. cheopis* fleas have been found in spite of thorough searches. Since the bubonic and septicaemic forms of plague need a vector organism (most likely an insect) to transmit the infection from one mammal to another, an important question is whether there are insect species that could have been responsible for transmission during medieval times in northern Europe. Many species of insects and arachnids, including lice, ticks and in particular various species of fleas, are suspected of being capable of transmitting plague between different mammalian species. Of these, only the human flea *Pulex irritans* and the human body louse *Pediculus humanus humanus* could possibly have been present in all European countries and in sufficient numbers to be real candidates during ancient human epidemics. In the report from the plague in Glasgow in 1900 quoted above we can read, "The homes/of the plague victims/consisted of a single room kept in a dirty, unventilated and overcrowded state, and swarming with vermin." In most modern epidemics where no *X. cheopis* have been identified, large numbers of the human flea *P. irritans* and/or the human louse *P. humanus* have been found instead (Baltazard and Seydian, 1960; Delanoë, 1925, 1932; Eskey, 1930; Blanc and Baltazard, 1942; Beasley, 1965; Laudisoit et al., 2007; Karimi et al., 1974).

An alternative transmission model for plague epidemics was published as early as the 1940s by plague experts Blanc and Baltazard at the Insitut Pasteur. This was based on field studies of plague epidemics in North Africa and Iran and on experimental work with fleas (Blanc and Baltazard, 1942, 1941). The French researchers found no traces of rats or rat fleas in either area, but they did find large numbers of human fleas and human body lice in clothes and bedding belonging to the nomadic peoples living there (Baltazard and Seydian, 1960; Blanc and Baltazard, 1942).

Experimentally, they showed that both *P. irritans* and *P. humanus* obtained from dying human plague victims contained *Y. pestis*. They also showed that *P. irritans* was capable of transmitting plague from dying human plague victims to guinea pigs and rats, and that *Y. pestis* could remain alive and virulent in soil (Mollaret, 1963). On the basis of these epidemiological and experimental studies, WHO plague expert Pollitzer concluded as follows in 1960: "– in areas [...] where [...] thick layers of clothing and lack of cleanliness tend to increase human infestation with ectoparasites, *P. irritans* is apt to take an important part in the transmission of plague –" (Pollitzer, 1960). Drancourt and Raoult's research group in Marseille have shown experimentally that *P. humanus humanus* can effectively transmit plague from rabbits infected with *Y. pestis* to uninfected rabbits (Houhamdi et al., 2006; Ayyadurai et al., 2010). The research group has also reconfirmed long-term persistence of *Y. pestis* in soil, for example in burrows dug by small mammals (Ayyadurai et al., 2008). Such animals are currently the most important reservoirs of infection for plague in the US (Colorado, Utah, Arizona and New Mexico), in South America (particularly Brazil, Peru, Bolivia and Ecuador) and in Kazakhstan (Stenseth et al., 2008). Historically, there may have been similar reservoirs of infection in Europe.

In 1914, Bacot and Martin published a seminal work describing how the proventriculus of infected rat fleas (*X. cheopis*) often becomes filled with a jelly-like mass of clotted blood and bacteria that blocks the oesophagus (Bacot and Martin, 1914). They showed that "blocked" fleas were effective transmitters of plague, probably because they remained hungry and constantly searched for new hosts from which to suck blood. Subsequent studies showed that in many other flea species, including the human flea *P. irritans*, blocking rarely occurs. It was therefore concluded that these species will be less effective at transmitting plague. Once the blockage has formed, which generally does not happen until 12–16 days after it has fed, *X. cheopis* transmits the disease very effectively, but only for a few days, because a completely blocked flea will die within five days. Unblocked fleas do not transmit plague as effectively during this particular period. However, unblocked fleas can live with the infection for a long time, in some cases many weeks. Rebecca Eisen and her co-workers at the Center for Disease Control and Prevention in Colorado have studied how efficiently plague is transmitted by flea species that do not become blocked (Eisen et al., 2006; Eisen et al., 2009; Eisen and Gage, 2012; Eisen et al., 2012). They used mice and the flea *Oropsylla montana*, which does not become blocked, and is the main vector from animals to humans in North America. The experiments showed that *O. montana* transmitted plague more effectively than *X. cheopis* in the first four days after infection, and that it remained effective long after the infected *cheopis* fleas had died. These experiments were concluded after eight weeks, but the authors assume that the fleas can remain infectious for longer than this. They also suggest that the results can be extrapolated to *P. irritans*.

4. Conclusion

What conclusions can be drawn concerning the transmission of earlier plague epidemics in Europe on the basis of recent biological research? Both the epidemics during the Justinian pandemic (542–767) and the European epidemics from 1347 onwards were plague epidemics, in other words caused by *Y. pestis*. During these epidemics in Europe, plague was transmitted directly from human to human by an insect ectoparasite vector, without a mammalian vector such as the black rat. The only potential candidates that were widely distributed in large numbers in all European countries appear to have been the human flea *P. irritans* and the human louse *P. humanus*. There were probably very large numbers of fleas and lice in people's clothes and bedding in the Middle Ages and early modern times. Over longer distances, plague was carried by people making journeys or in the goods they transported. Infected human fleas can survive for long periods without feeding, and could therefore have been transported in clothing, wool and many other types of goods. This transmission model, unlike the rat model, can also explain the rapid spread of plague epidemics. It also explains why all members of one household in a town might become plague victims while neighbouring households escaped. Many such cases were observed, and they cannot be explained by the rat model, since the territory of a rat colony in a medieval town would extend across a number of buildings. Black rats could not have been involved in the transmission of plague in Northern Europe, and probably not in more southerly parts of Europe either (Rodenwaldt, 1953). In contrast, black rats were an important vector of plague in South China before 1894 (and at least as far back as the 1600s), in Hong kong in 1894, in many (but not all) parts of India after 1896, and in cities such as Alexandria and Sydney about 100 years ago (and in Madagascar and East-Africa today). The plague epidemics in all these areas spread slowly.

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