

## Feature Review

# Interspecies transmission and emergence of novel viruses: lessons from bats and birds

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**As exemplified by coronaviruses and influenza viruses, bats and birds are natural reservoirs for providing viral genes during evolution of new virus species and viruses for interspecies transmission. These warm-blooded vertebrates display high species biodiversity, roosting and migratory behavior, and a unique adaptive immune system, which are favorable characteristics for asymptomatic shedding, dissemination, and mixing of different viruses for the generation of novel mutant, recombinant, or reassortant RNA viruses. The increased intrusion of humans into wildlife habitats and overcrowding of different wildlife species in wet markets and farms have also facilitated the interspecies transmission between different animal species.**

## Emergence of new viruses

Both mammalian and avian coronaviruses (CoV) have diverse host ranges. Phylogenetic dating of RNA-dependent RNA polymerase (RdRp) sequence divergence suggested that the most recent common ancestor (MRCA) of mammalian CoVs appeared around 7000–8000 years ago, whereas the MRCA of avian CoVs dates back to 10 000 years ago (Figure 1). These results are likely underestimations because they could not account for additional sequence diversity from undiscovered viruses. Nonetheless, the present estimates roughly coincide with the dispersal of the human population around the world about 50 000–100 000 years ago and greatly increased in the last 10 000 years during the first historic transition. During this transition, humans began various farming activities, such as forest clearing for agriculture and animal herding, leading to a significant shift in the ecology and population dynamics of viruses owing to the intrusion of wildlife habitats and intensive mixing of different animal hosts. Finally, the expansion of

human travel and trading directly led to the spread of viruses to distant and isolated places. The migration of early humans over long distances was very limited and effectively a unidirectional ‘rare’ event. Eventually, improvements in transportation technology enabled distant trade missions in early Mesopotamia around 5000 years ago and possibly earlier in other regions [1]. These periodic yet infrequent visits might have enabled transmission of various disease agents to previously segregated non-immune populations, leading to a serial founder effect associated with a boom and bust cycle. However, further technological improvements, especially the development of aviation and the flight industry in the last century, have allowed this type of travel to occur at such high frequencies that multiple segregated host populations effectively have become a single large population. These changes coincided with increased breeding between different host populations (for both humans and domestic animals), which can significantly impact the genetic and immunological make-up of the host populations. When these occurrences are considered in the context of the high mutation rate of RNA viruses, they become a driving force for speciation and subsequent evolution of new viruses. Although phylogenetic analysis and dating of individual influenza genes and lineages have been reported previously, large sequence divergence and frequent reassortment led to difficulties in precisely dating and phylogenetic positioning the common ancestor of modern influenza viruses [2].

About 70% of the emerging pathogens infecting humans originate from animals. Most of these major outbreaks were due to RNA viruses as a result of their higher mutation rates compared with other types of microbes and their capability for unique genetic change, either by genetic recombination in positive-sense RNA viruses or genetic reassortment in RNA viruses with segmented genomes. Those with greatest impact on humans include the severe acute respiratory syndrome coronavirus (SARS-CoV), influenza virus, and HIV. Little was known about CoVs until the 2003 SARS epidemic, which caused 774 deaths among 8098 cases in over 30 countries [3]. The natural reservoir of

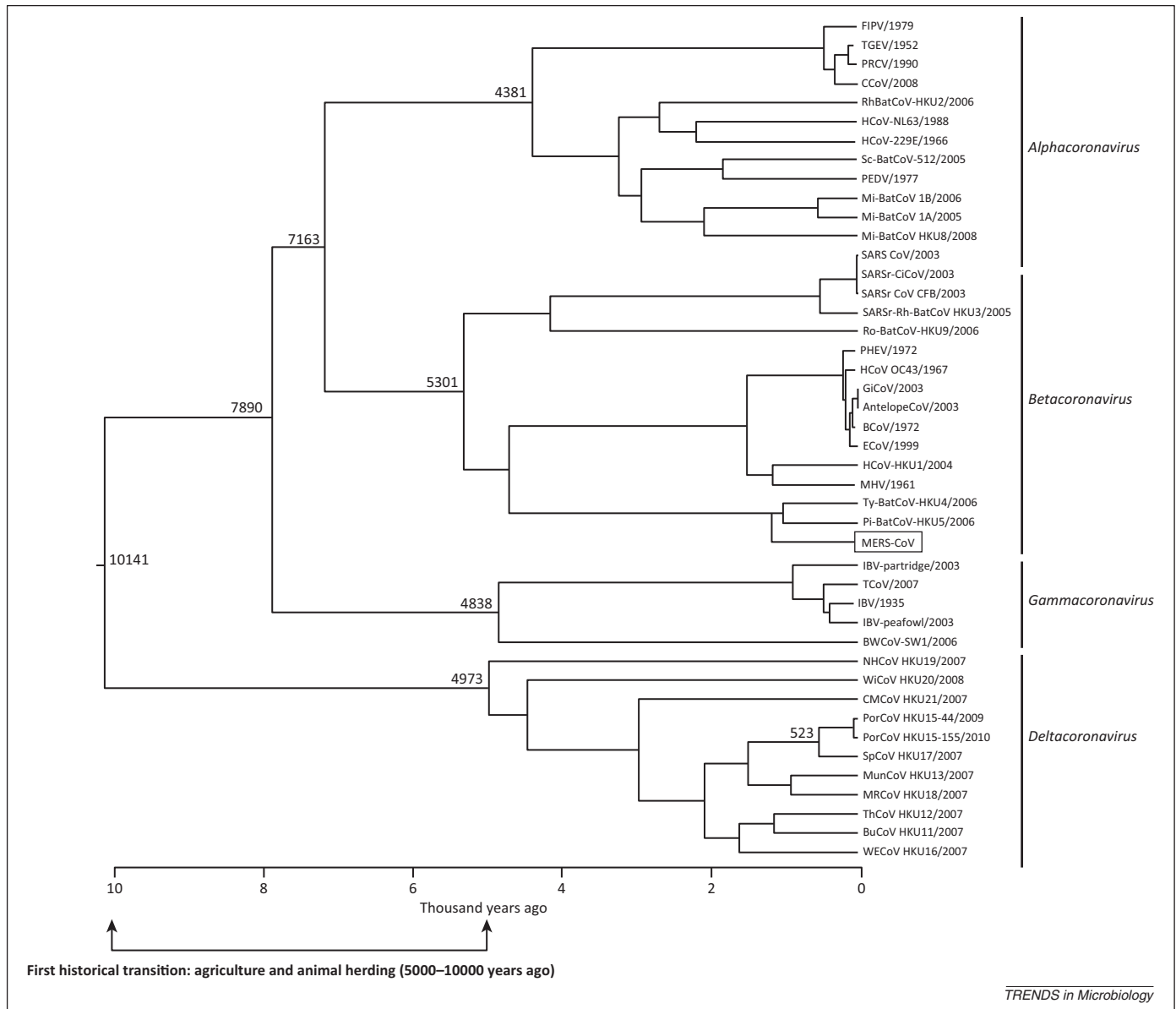
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**Figure 1.** The divergence of coronaviruses into *Alphacoronavirus*, *Betacoronavirus*, *Gammacoronavirus*, and *Deltacoronavirus* is estimated to have occurred approximately 5000 years ago. This tree was generated by analyzing RNA-dependent RNA polymerase (RdRp) genes under the relaxed-clock model with an uncorrelated log-normal distribution in Bayesian evolutionary analysis sampling trees (BEAST) software. Values at branch points represent the estimated timing of divergence events in numbers of years before the present. Adapted from [45].

the more ancestral bat SARS-CoV is the Chinese horseshoe bat (*Rhinolophus sinicus*), which may have transmitted the virus to other game mammals including Himalayan palm civets (*Paguma larvata*), raccoon dogs (*Nyctereutes procyonoides*), and Chinese ferret badgers (*Melogale moschata*) in wildlife markets in South China [4]. This finding sparked intense hunting for novel CoVs in humans and different animal species, especially in bats. The latest emerging novel human CoV, originally named human coronavirus EMC/2012 and later renamed Middle East respiratory syndrome coronavirus (MERS-CoV), which has caused 30 deaths among 54 cases in the Middle East, Europe, and Africa, is also phylogenetically closely related to the *Tylonycteris* bat CoV HKU4 (Ty-BatCoV-HKU4) and *Pipistrellus* bat CoV HKU5 (Pi-BatCoV-HKU5) discovered in bats in Hong Kong [5–8] ([http://www.who.int/csr/don/2013\\_06\\_05/en/index.html](http://www.who.int/csr/don/2013_06_05/en/index.html)). The importance of birds as

natural reservoirs of emerging influenza viruses is underscored by the persistent threat of avian influenza H5N1 since 1997 and the emergence of H7N9 in 2013 [9–12]. The role of bats in the emergence of novel influenza viruses is less clear although influenza A H17 and H3N2 viruses have been discovered in *Sturnira lilium* recently and in *Nyctalus noctula* bats in Kazakhstan in 1970, respectively. We review the importance of bats and birds in the genesis of new virus mutants and interspecies jumping using CoVs and influenza viruses as examples.

### Bats as natural reservoirs for emerging viruses

A number of unique ecological, biological, immunological, and genetic features make bats a favorable animal reservoir for the emergence of novel viruses. Bats have remarkable species diversity, with over 1240 species (20% of the nearly 5000 known species within Mammalia and only

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