

Papers in Honour of Ken Aplin

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Evolutionary History of the Subgenus *Mus* in Eurasia with Special Emphasis on the House Mouse *Mus musculus*

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ABSTRACT. Elucidation of the evolutionary history of the subgenus *Mus*, including the House Mouse *Mus musculus*, is essential to understanding species diversification mechanisms in the Indomalayan region, which is a global biodiversity hotspot. In terms of interspecific relationships, the topography of India, Myanmar, and other Southeast Asian regions has been proposed to explain the speciation process and ecological niche diversification followed by range overlap after speciation. Recent research into mitochondrial DNA clocks has created the opportunity to reconstruct the detailed dynamics of *M. musculus* as affected by human activity. The resultant evolutionary scenarios are in good accordance with archaeological evidence observed in Asia, especially in China, Korea, and Japan.

Introduction

The evolution of murine rodents (subfamily Murinae) is the most successful example of species diversification in mammals (Musser & Carleton, 2005). Over 560 species emerged within a short evolutionary time of several million years (Myr), with an unusual level of morphological diversity. The genus *Mus*, which includes the well-known model species, the House Mouse *Mus musculus*, is a species-rich group of murine rodents with unclear taxonomic diversity, probably due to substantial morphological similarity among species. Ken Aplin, a researcher who undertook extensive field studies in Southeast Asia to control pest rats and mice (Aplin, 2003), has expanded the network of researchers committed to resolving the taxonomic relationships of rats and mice and describing their evolutionary histories using genetic methods (e.g., Aplin *et al.*, 2011). In this article, I focus on his findings in studies of *Mus* species over the last two decades, and review the recent progress of phylogenetic research into members of the subgenus *Mus* and phylogeographic studies of the widespread species *M. musculus*.

Framework of species diversity in the subgenus *Mus*

The genus *Mus* dominates the small granivore/omnivore niche in the Old World region from southern Africa to eastern Asia, and is now recognized as comprising more than 40 species (Musser & Carleton, 2005; Shimada *et al.*, 2010). In Eurasia, 20 species of *Mus* are known, which are grouped in the subgenus *Mus*. The taxonomy of this group was relatively stable until field surveys (2003–2007) of mice from Myanmar by Ken Aplin. He noticed taxonomic problems among the mice from Myanmar and conducted genetic studies to determine their phylogenetic backgrounds. In his research, populations previously known as *Mus cervicolor* and *Mus booduga* were found to have distinct evolutionary histories from mice referred to as *Mus cervicolor* from Thailand and Laos, and those called *Mus booduga* from India and Nepal, respectively. He demonstrated that the appropriate taxonomic names for these mice were instead *Mus nitidulus* Blyth, 1859 (Shimada *et al.*, 2007a) and *M. lepidoides* Fry, 1931 (Shimada *et al.*, 2010), respectively, characterizing them as

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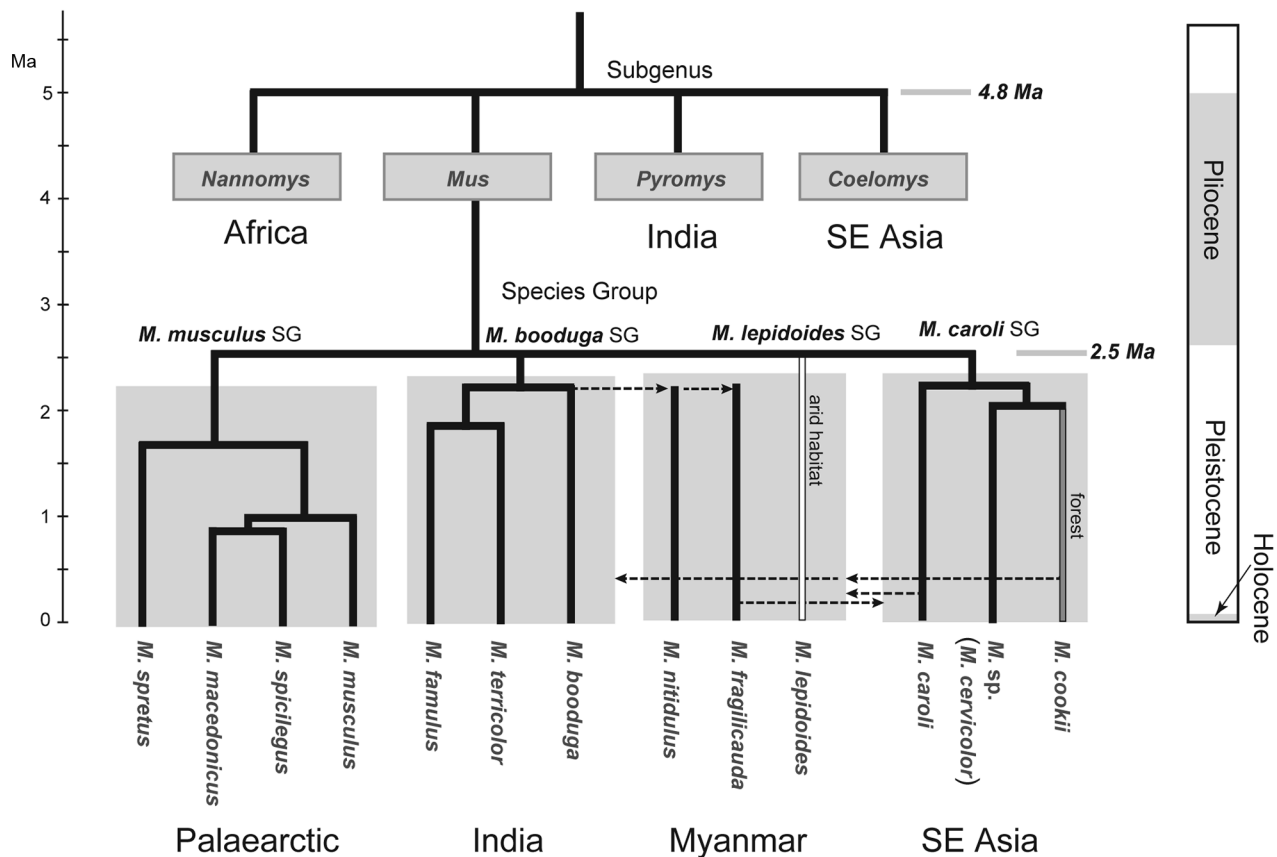


Figure 1. A sketch of the evolutionary patterns of lineage differentiation among species in the genus *Mus* based on molecular phylogenetic analysis of nuclear gene sequences (Suzuki *et al.*, 2004; Shimada *et al.*, 2010). The tree shows the four subgenera of the genus *Mus* and the four species groups (SGs) of the subgenus *Mus*: *M. musculus*, *M. booduga*, *M. lepidoides*, and *M. caroli* (previously termed as *M. cervicolor* SG), representing four geographic regions of the Palaeartic region, Indian subcontinent, Myanmar, and Southeast Asia, respectively. The taxon previously regarded as “*M. cervicolor*” in Thailand is here referred to as “*M. sp.*”, due to uncertainty regarding the taxonomic status of the sampled specimens (see main text). The estimated divergence times for the subgenera and species groups are approximately 5 and 2.5 million years ago, respectively (Shimada *et al.*, 2010). Specific habitat transitions from grasslands to forests and arid areas are marked for the species lineages of *M. cookii* and *M. lepidoides*. Predicted dispersal events between geographic regions are indicated with dotted arrows.

valid species endemic to Myanmar. The elucidation of these two additional species in the subgenus *Mus* from Myanmar led to two important findings. First, the region of Myanmar is an important zoogeographic area for understanding the species diversity of the subgenus *Mus*. Second, our current understanding of the taxonomy and phylogenetic status of the subgenus *Mus* and its distribution is incomplete, and therefore further intensive study is necessary.

A preliminary framework of the evolutionary history of the genus *Mus*, especially for members occurring in Eurasia, has been inferred based on molecular phylogenetic analyses (Fig. 1; e.g., Suzuki *et al.*, 2004). The genus *Mus* is classified into four subgenera (Marshall, 1977), with equal evolutionary distances among all, including Southeast Asian (*Coelomys*), Indian subcontinent (*Pyromys*), African (*Nannomys*), and Palaeartic (*Mus*) lineages (Lundrigan *et al.*, 2002; Suzuki *et al.*, 2004; Chevret *et al.*, 2005; Tucker *et al.*, 2005; Veyrunes *et al.*, 2005; Shimada *et al.*, 2007a, 2010). The species-rich Eurasian subgenus *Mus* was found to have four distinct species groups (SGs): (1) the *M. caroli* SG (mainland Southeast Asian clade) including *M. caroli*, *M. cervicolor*, and *M. cookii*; (2) the *M. musculus* SG (Palaeartic clade) with *M. musculus*, *M. spretus*, *M.*

spicilegus, and *M. macedonicus*; (3) the *M. booduga* SG (Indian clade) containing *M. booduga*, *M. terricolor*, *M. famulus*, *M. nitidulus*, and *M. fragilicauda*; and (4) the *M. lepidoides* SG, a monospecific clade endemic to Myanmar. The distribution pattern of the four species groups suggests origins in each of the four geographic regions of the Indomalayan Realm (Suzuki *et al.*, 2014; Shimada *et al.*, 2010). Their phylogenetic patterns can be characterized by two prominent divergence periods—for the four subgenera, and for the four species groups (Suzuki *et al.*, 2004; Shimada *et al.*, 2010; Suzuki & Aplin, 2012). These two historical periods occurred 5–6 million years ago (Ma) and 2–3 Ma, respectively, based on molecular phylogenetic analysis and fossil evidence of rat and mouse bifurcation (at 12 Ma). These periods coincide with global environmental changes at the boundaries of the Miocene/Pliocene and Pliocene/Pleistocene, respectively. Intermittent dramatic changes in the global environment played an important role in the diversification of *Mus* species (Fig. 1).

The distribution ranges of Eurasian mice remain poorly understood, especially those of the two recently recognized species (*M. nitidulus* and *M. lepidoides*) in Myanmar. A team from the University of Yangon, Myanmar, led by Thidalay

They performed a field survey to clarify the distribution ranges of mouse species in Myanmar, including *M. nitidulus* and *M. lepidoides* (Myat Myat Zaw *et al.*, 2019). They found that *M. nitidulus* has a wide habitation zone along the Ayeyarwady River. Surprisingly, they observed *M. fragilicauda* in Pyay city, where it was restricted to the eastern side of the Ayeyarwady River. Myanmar is still expected to reveal new species of forest mice (subgenus *Coelomys*) and grassland mice (subgenus *Mus*). Moreover, an important finding of the field study is that no specimens of *Mus* from Myanmar were found to be genetically closely related to samples identified as *M. cervicolor* in studies of that species from Thailand, i.e. based on sequences of mitochondrial DNA (cytochrome *b*, *Cytb*) or nuclear DNA (melanocortin 1 receptor, *Mclr*) (Myat Myat Zaw *et al.*, 2019). This finding does not support the view that *Mus cervicolor*, which was first described from Nepal, is distributed broadly from Nepal to Vietnam (e.g., Wilson *et al.*, 2016). Little molecular phylogenetic or morphological analysis has been conducted with Nepalese mice, and thus *Mus cervicolor* from Thailand may not represent the original *Mus cervicolor*, first described from Nepal. Therefore, it is reasonable to treat these mice from Thailand temporarily as “*Mus* sp.”, as the species identity is unclear.

Reconstructing the diversification history of mouse species

Here, I address the possible evolutionary scenarios and factors shaping the speciation events among the 13 species in the subgenus *Mus* (Fig. 1). The *M. booduga* SG consists of five species: *M. booduga*, *M. terricolor*, *M. famulus*, *M. nitidulus*, and *M. fragilicauda*. The ancestral lineage extended its range from a predicted home range on the Indian subcontinent into Myanmar around 2 Ma (2 million years ago), creating the *M. nitidulus* species lineage. Simultaneously, the lineage further dispersed to the east, forming *M. fragilicauda*, somewhere in Southeast Asia. *Mus fragilicauda* currently has a fragmented distribution in Thailand, Laos, and Myanmar, within which lineage divergence is estimated to have occurred around 400,000 years ago (Myat Myat Zaw *et al.*, 2018). This distribution pattern may be explained by dispersal following Pleistocene climatic fluctuation or fragmentation due to range extension of competing species as has been suggested in other studies on small mammals (e.g., Honda *et al.* 2019).

Mus lepidoides, the sole member of the *M. lepidoides* SG, has been collected by Ken Aplin from the Central Dry Zone of Myanmar. To date, the full range of this species has not been reported, although it is likely within the arid region of central Myanmar. Future work must investigate the distribution of *M. lepidoides* and the biogeographic effects of the Ayeyarwady River, which flows through the centre of Myanmar, on the genetic differentiation of this arid-adapted species.

In Southeast Asia, the *caroli* SG diverged into three lineages, leading to the species *M. caroli*, *M. cookii*, and *Mus* sp. (formerly “*M. cervicolor*”, found in Thailand), in Southeast Asia around 2.4 Ma. *Mus caroli* and *Mus* sp. may have evolved on the western and eastern plains of the Indochina peninsula, while *M. cookii* adapted to forest dwelling in more northern forested areas (Fig. 1), and extends as far west as the Himalayan foothills region

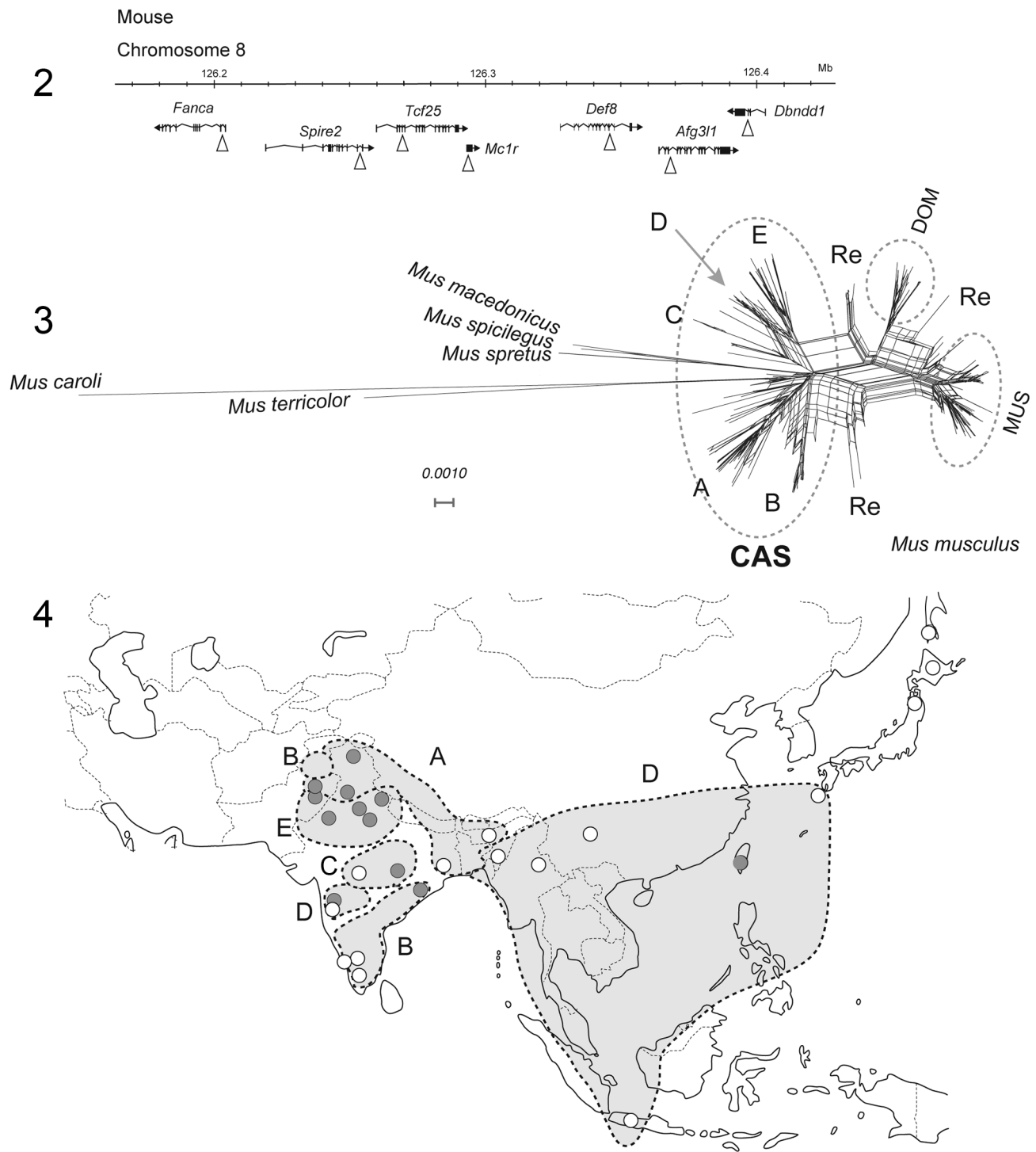
of Pakistan (Bibi *et al.*, 2017). The remaining species are grassland dwellers, and their speciation can be explained through geographic segregation, or stratification of shared distributions, after niche differentiation. *Mus caroli* has a wide range from Myanmar to Taiwan, containing several distinct geographic lineages (Shimada *et al.*, 2007b). It may have extended its distribution westward during the Chibanian (c. 500,000–400,000 years ago), accounting for the level of genetic divergence among geographic groups (Fig. 1).

The *musculus* SG has four member species: *M. spretus*, *M. macedonicus*, *M. spicilegus*, and *M. musculus*, with estimated divergence in the period 1.7–1.4 Ma (Suzuki *et al.*, 2013; Kodama *et al.*, 2015). Aside from *M. musculus*, the other species are currently parapatric. This group may have expanded its range around 1.7 Ma and then diverged into the four species in different geographic areas, with *M. musculus* probably representing the easternmost part of the species group’s range. *Mus musculus* has five main mtDNA lineages (Sakuma *et al.*, 2016), with estimated divergence times of 400,000–500,000 years ago, but regional differentiation could have started at least one million years ago (Kodama *et al.*, 2015). Hence, it is possible that *M. musculus* gained genetic diversity by occurring in multiple geographic regions at the beginning of the speciation process of the *musculus* SG.

Widespread development of the mouse on the Eurasian continent during the prehistoric period

Environmental changes during the Pleistocene had a great impact on the differentiation and spatial dynamics of *Mus* species. The last 15,000 years, including the terminal Pleistocene and Holocene, are characterized by an interglacial climate and widespread anthropogenic environmental impacts. Anthropological influences on evolution have been well documented, including on the dramatic spatial expansion and extensive hybridization events among the three subspecies groups of *M. musculus* (e.g., Nunome *et al.*, 2010). A similar trend can be observed in the commensal species of *Rattus* (Aplin *et al.*, 2011). The Brown Rat (*R. norvegicus*) and Black Rat (*Rattus rattus* complex) are distributed widely in colder and warmer regions, respectively. *Mus musculus* is found in both ranges, and hence has been characterized as the most successful rodent due to its global distribution, with exceptions in urban areas and regions where congeneric species occur densely. The House Mouse may have special ecological traits that allow the species to inhabit human-made environments. For example, in addition to using underground spaces for their nests, they find suitable structures on the ground (e.g., timber gaps) for accommodation and use human houses for shelter from cold weather or competition from congeneric species. Here, I summarize the evolutionary history of *M. musculus* before and after the major human-associated range expansion events.

The original range of *M. musculus* is thought to be in the Middle East and Indian subcontinent (Boursot *et al.*, 1993). This origin is supported by the presence of region-specific mtDNA lineages in Nepal and the southern tip of the Arabian Peninsula. Kodama *et al.* (2015) analysed genetic variation in seven linked nuclear gene sequences on chromosome 8 in mice collected from a broad area of Eurasia including India and Pakistan, within the native range (Figs 2–4), and found that *M. musculus* can be divided into three subspecies groups,



Figures 2–4. Assessment of population genetic structure using concatenated sequences (4302 bp) of seven nuclear genes. (2) Positions of the analysed regions (open triangles) in seven genes on murine chromosome 8 (Nunome *et al.*, 2010; Kodama *et al.*, 2013). (3) Neighbour-Net network based on concatenated sequences from 98 *Mus musculus*, showing haplogroups representing the subspecies groups *Mus musculus domesticus* (DOM), *Mus musculus castaneus* (CAS), and *Mus musculus musculus* (MUS) as well as recombinant haplotypes (Re) (Kodama *et al.*, 2013). In the network, the level of diversity of CAS is markedly higher than those of DOM and MUS, yielding five distinct phylogroups A–E. Scale bar indicates genetic divergence. (4) Approximate geographic ranges of the five subclusters of CAS. Localities where samples used in this analysis were collected are marked with open and filled circles, representing the mitochondrial haplogroup CAS-1 and all other types, respectively (Kodama *et al.*, 2013). The phylogroups A–E of CAS showed rough geographical distributions and one of them, phylogroup D, comprised the haplotypes recovered from a large geographical area of Southeast Asia, south China, and Indonesia and can be characterized as the lineage dispersed with prehistoric human movement (arrow; Kodama *et al.*, 2015). Note that subcluster D (arrow in Fig. 3) shows a broad distribution range in Southeast Asia and the southern part of East Asia. In the Neighbor-Net network, this subcluster exhibits limited divergence among haplotypes.

M. m. domesticus (DOM), *M. m. musculus* (MUS), and *M. m. castaneus* (CAS). The levels of differentiation vary among the nuclear genes examined and some genes show more ancient divergence of allelic sequences than others, up to 1 Ma (Kodama *et al.*, 2015). The three subspecies groups may have had genetic exchanges prior to their human-associated geographical expansion (Kodama *et al.*, 2015). In addition, hybridization among subspecies groups has occurred due to secondary contact after long-distance dispersal, and hence the composition of the nuclear genome of *M. musculus* is complex (Nunome *et al.*, 2010; Kuwayama *et al.*, 2017). However, the rapidity of evolution of these nuclear genes allows reconstruction of this complexity of each subspecies group's range expansion events.

Of the three subspecies, DOM, which is currently found in Western Europe, showed a star-like structure in the network constructed from mtDNA sequences (*Cytb*, 1140 bp), indicative of rapid population expansion. The mode of the number of substitutions among the sequences (τ) is around 5.6 (Suzuki *et al.*, 2013). The time (T) when expansion started can be calculated as 52,000 years ago ($T = 5.6/2/1140/4.7/10^{-8}$) based on the time dependent evolutionary rate of 0.047 substitutions/site/Myr (see Hanazaki *et al.*, 2017 for detail). During this period, major environmental changes have occurred, with rapid expansion of grasslands in the Northern Hemisphere. Moreover, a simultaneous population expansion of herbivorous rodents (voles, genus *Myodes*) has been observed in North America (Kohli *et al.*, 2015), the Eurasian continent (Abramson *et al.*, 2012), and the Japanese archipelago (Honda *et al.*, 2019). The DOM subspecies group is believed to have expanded its geographic range into Western Europe approximately 15,000–10,000 years ago based on fossil evidence (Cucchi *et al.*, 2005; Weissbrod *et al.*, 2017). In my view, this range expansion event more likely occurred before this time range, with nucleotide diversity achieved prior to the human-associated expansion, if we accept that the generation of diversity began around 50,000 years ago in its original range. Notably, historical colonization is not always associated with development of an agricultural system and has also been achieved by human settlements without agriculture (Weissbrod *et al.*, 2017). In modern times, DOM continues to be introduced to other parts of the world (e.g., Indonesia, Senegal, Somalia, Australia) (Suzuki *et al.*, 2013). In contrast, Russian DOM populations have unique features and are suggested to have arisen from a different historical episode. In Japan, haplotype structure analysis of nuclear genes indicated that DOM has been introduced very recently, perhaps 50 years ago (Nunome *et al.*, 2010; Kuwayama *et al.*, 2017; Isobe *et al.*, 2018). A DOM fragment of approximately 3–5 Mb is embedded in the nuclear genome of Japanese mice, with an estimated transfer time several decades ago (Nunome *et al.*, 2010; Kuwayama *et al.*, 2017; Isobe *et al.*, 2018).

The subspecies group MUS has a huge range in northern Eurasia. Notably, morphological features differ substantially between mice in Eastern Europe and East Asia (Marshall, 1998). Based on morphological characters and genetic analyses, the subspecies group can be subdivided further into two groups, MUS-I and MUS-II, represented by the traditional subspecies of “*M. m. musculus*” and “*M. m. wagneri*”, respectively, which may have originated in separate geographic areas, such as the western and eastern

sides of the Caspian Sea (see Suzuki *et al.*, 2015). In mtDNA variation analysis, two phylogroups, termed MUS-1 and MUS-2, were recognized, with an estimated divergence time of 130,000 years ago (Suzuki *et al.*, 2013). These phylogroups tend to be distributed in the southern and northern parts of Eurasia, respectively. Applying the time-dependent evolutionary rate of 0.11 substitutions/site/Myr for inference of divergence times based on mtDNA sequences led to detailed reconstruction of *M. musculus* dynamics, as affected by human activity (Suzuki *et al.*, 2013; Kuwayama *et al.*, 2017). The resultant evolutionary scenarios are in good accordance with archaeological evidence observed in Asia, especially in China, Korea, and Japan (Li *et al.*, 2020).

CAS contains three or four major mtDNA sub-lineages that diverged hundreds of thousands of years ago; among them, CAS-1 has spread over a wide area of eastern Eurasia (Figs 3C, 4). It extends to many regions of South and East Asia, including Pakistan, India, Southeast Asia, Indonesia, Philippines, south and northeast China, Primorye, Sakhalin, and Japan (Suzuki *et al.*, 2013; Kuwayama *et al.*, 2017; Bibi *et al.*, 2017). The network drawn from CAS-1 haplotypes has a star-shaped structure, indicative of rapid population expansion events. The beginning of rapid expansion was calculated as 8000–7000 years ago (Suzuki *et al.*, 2013; Kuwayama *et al.*, 2017), based on the time-dependent mtDNA evolutionary rate of 0.11 substitutions/site/Myr. This date is consistent with early agricultural development in Asia (Fuller *et al.*, 2010, 2014). In addition, a secondary expansion event occurred in south China, as observed in the basin of the Yangtze River including localities in Yunnan (Lijiang, Dali, and Kunming), as well as in Kyushu, Tohoku, and Hokkaido, in Japan (CAS-1a). The initiation of this expansion was estimated at around 4000 years ago. More detailed analysis, such as investigation of whole mitochondrial DNA sequences, is needed.

Conclusion

The direction of research on the taxonomic and molecular phylogenetic relationships of the murine subfamily in Southeast Asia was initiated by Ken Aplin twenty years ago. He constructed a framework of the phylogenetic relationships among species in the genus *Mus* (Shimada *et al.*, 2010) and demonstrated the need for analysis of intra-species geographic variations through the examples of *M. musculus* (Suzuki *et al.*, 2013) and *M. caroli* (Shimada *et al.*, 2007). At present, the research that he began is being continued by his colleagues and progressing toward its goal, despite many aspects remaining unexplained. In particular, it is necessary to carefully examine the species status of “*Mus cervicolor*” throughout its putative range. In Myanmar, research addressing species assemblages is in progress and early signs suggest that new species exist, for which both morphological and molecular studies are necessary. Another important issue involves resolving the impact of humans on the diversity of rodents in the human era of the last 15,000 years. Such efforts will serve to clarify the concealed evolutionary history of these species in prehistory. Ken Aplin conducted a survey of the black rat, *Rattus rattus* complex, using mtDNA sequences and characterized the general movements of the species complex in Eurasia (Aplin *et al.*, 2011). Ken Aplin also conducted surveys worldwide using nuclear markers for

the *R. rattus* complex that are still currently being worked on. To attain a comprehensive view of the impacts of human history on rodent evolution, comparative studies should be conducted on other commensal rodents in addition to the *R. rattus* complex and *M. musculus* (Aplin & Singleton, 2003), such as *R. exulans* (Thomson *et al.*, 2014) and *Bandicota* species (Pagès *et al.*, 2010). Clarification of evolutionary trends based on mtDNA markers is an important step toward reaching this goal.

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