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Solving the 250-year-old mystery of the origin and global spread of the German cockroach, *Blattella germanica*

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The origin of the German cockroach, *Blattella germanica*, is enigmatic, in part because it is ubiquitous worldwide in human-built structures but absent from any natural habitats. The first historical records of this species are from ca. 250 years ago (ya) from central Europe (hence its name). However, recent research suggests that the center of diversity of the genus is Asian, where its closest relatives are found. To solve this paradox, we sampled genome-wide markers of 281 cockroaches from 17 countries across six continents. We confirm that *B. germanica* evolved from the Asian cockroach *Blattella asahinai* approximately 2,100 ya, probably by adapting to human settlements in India or Myanmar. Our genomic analyses reconstructed two primary global spread routes, one older, westward route to the Middle East coinciding with various Islamic dynasties (~1,200 ya), and another younger eastward route coinciding with the European colonial period (~390 ya). While Europe was not central to the early domestication and spread of the German cockroach, European advances in long-distance transportation and temperature-controlled housing were likely important for the more recent global spread, increasing chances of successful dispersal to and establishment in new regions. The global genetic structure of German cockroaches further supports our model, as it generally aligns with geopolitical boundaries, suggesting regional bridgehead populations established following the advent of international commerce.

domestication | globalization | insecticide resistance | integrated pest management | invasive species

The rise of human civilization has triggered the evolution and spread of commensal species adapted to urban environments. Some species have become invasive pests, with serious implications for human well-being and economic prosperity (1). Many of these pest species have spread globally, facilitated by human technological innovations, which include advancements in transportation and housing, notably plumbing and heating (2). A deeper understanding of the factors that facilitate the spread of pest species can help prevent further spread and mitigate future economic losses (3). However, tracing the spread of pests based on historical records is often obscured by a dearth of accurate record-keeping, especially prior to the 1950s (4). Advances in population genomics help trace origins and reconstruct spread routes when historical records are limited and geographically biased (4). The German cockroach, *Blattella germanica* L., the world's most prevalent cockroach pest, is ubiquitous in human buildings globally but not outdoors; it imposes significant social, medical, and economic costs (5) due to prevalent insecticide resistance allowing it to outcompete ~40 known pest cockroach species in buildings (6).

The origin and spread of the German cockroach are shrouded in mystery. Described by Linnaeus in 1776 about a decade after the Seven Years' War, historical records have suggested a global spread of German cockroaches from Europe between the late 19th to early 20th centuries (6). However, the German cockroach has no close relatives in Europe; those are in Africa and Asia. The ancestral species was suggested to be the Asian cockroach, *Blattella asahinai* Mizukubo (7, 8), native to the Bay of Bengal in Asia (east India, Myanmar, and nearby islands), and invasive in agricultural landscapes in the southern United States (7). The paradox of a European beginning but Asian phylogenetic affinity is likely due to the almost complete lack of systematic entomological knowledge across the world prior to the 20th century. To help fill the knowledge gap and solve this paradox, we used genome-wide markers from 281 samples from 17 countries around the world (Fig. 1), from which we described the genetic structure and reconstructed spread routes of the German cockroach.

Results and Discussion

Based on the 1,536 bp mitochondrial COI gene, we found a shallow divergence between Asian and German cockroaches (~0.59%; 9 bp), in stark contrast with the 10 times higher divergences with other congenerics, e.g., *Blattella bisignata* and *Blattella lituricollis*, (>5%; 92 bp and 84 bp respectively). German cockroaches from 83% (44/53) of sites had

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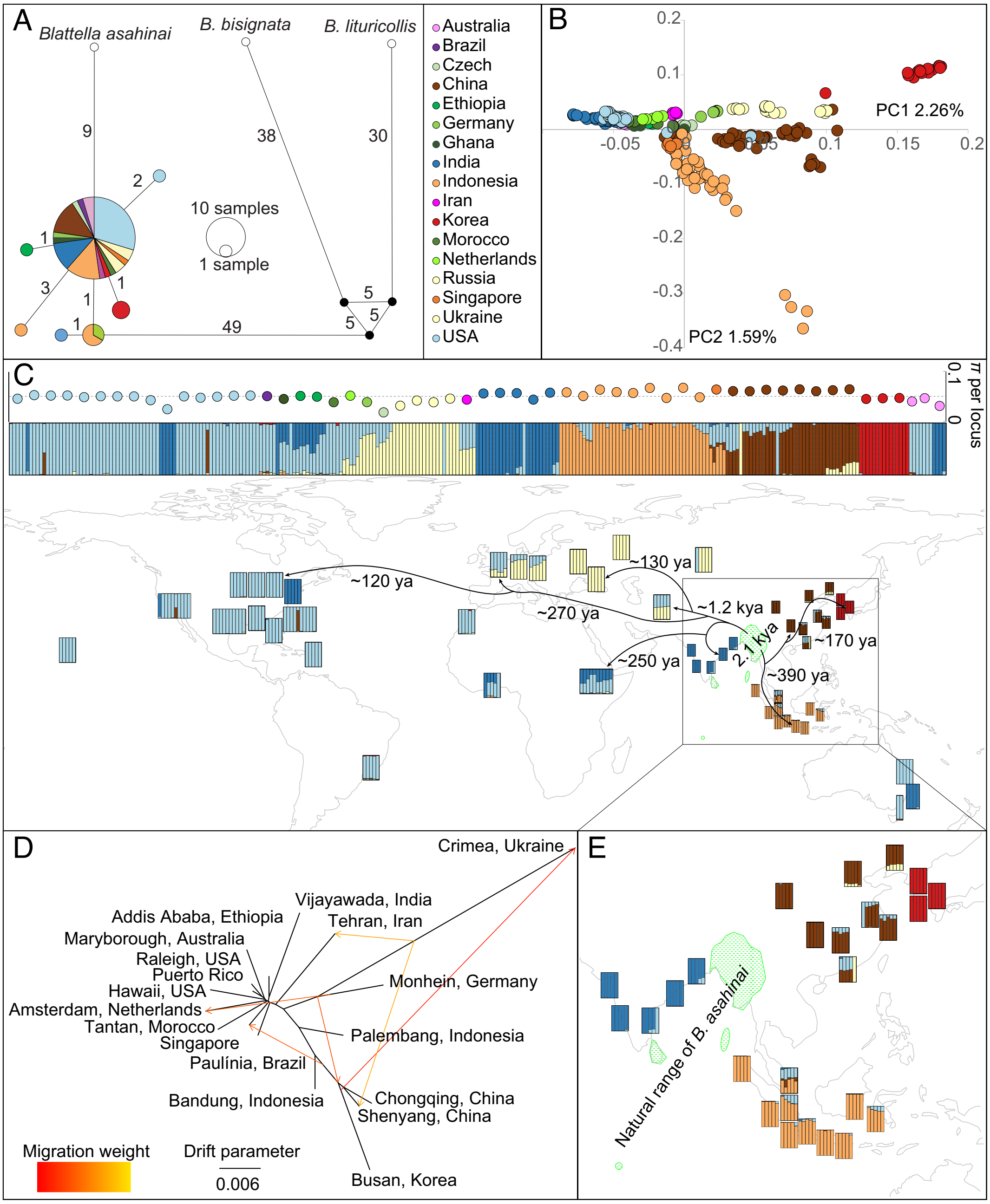

Fig. 1. Population genetic structure and global spread routes of the German cockroach, *Blattella germanica*. (*A*) Median joining haplotype network based on the COI gene (1,536 bp). (*B*) Principal component analysis based on 158,216 genome-wide single nucleotide polymorphisms. (*C*) Bar plot (*Top*), split into region-specific bar plots mapped to sampling sites, derived from maximum likelihood estimation of ancestry (ADMIXTURE) at the optimal number of ancestral clusters (K = 6). The diagram on top of the bar plot indicates nucleotide diversity (π) per locus at each sampling site. The inferred timing and routes of global spread are mapped with black arrows. (*D*) Divergence of key populations presented in the form of an allele-frequency-based unrooted tree with residuals of drift parameters mapped as migration edges. (*E*) A zoomed-in view of (*C*) focused on Asia. The natural range of the ancestor, *B. asahinai*, is shown in green.

identical haplotypes (Fig. 1*A*); the remainder had very low levels of differentiation (0.07 to 0.2%; 1 to 3 bp) between the minor and major COI haplotypes, indicating a recent origin and spread.

Further evidence for a recent global spread came from the limited population subdivision across the globe based on 158,216 single nucleotide polymorphisms (Fig. 1*B*). Maximum likelihood estimation of ancestry, implemented in ADMIXTURE v1.3 (9), suggested six major ancestral clusters of German cockroaches (Korea, China, Indonesia, India, Eastern Europe, and United States), which would have served as sources for modern global populations (Fig. 1*C*). Curiously, the highest divergence was among populations from Korea, Indonesia, and India in Asia even though these are close to the native range of their ancestor *B. asahinai* (7). Moreover, Asian populations (China, India, and Indonesia) exhibited a higher level of nucleotide diversity than other populations (Fig. 1*C*). Most samples from the same country/region shared ancestry, with a few exceptions revealing possible secondary introductions after the establishment of a regional bridgehead population (Fig. 1*C*). This is supported by the relatively high inbreeding within sampling sites (inbreeding coefficient, F_{IS}, from −0.12 to 0.65), along with low genetic differentiation between pairs of sampling sites (pairwise F_{ST}), ranging from 0 to 0.35. It is also apparent that regional ancestry may correspond to human commercial links. For example, German cockroaches in Singapore and Australia are more closely related to those in the United States than with geographically adjacent populations in Indonesia (Fig. 1 *C* and *D*).

We tested different scenarios of divergence among populations and reconstructed the spread routes of the German cockroach with individuals from nine selected sampling sites by comparing the observed site frequency spectrum with coalescence-based simulations [implemented using fastsimcoal2 v.2.7 (10)] (*SI Appendix*). Six of the nine selected sites (China, Indonesia, India, Korea, Ukraine, and USA) represented the six pure ancestries identified with ADMIXTURE (Fig. 1*C*); three sites represented wider regions (Ethiopia for Africa, Iran for Western Asia, and the Netherlands for Western Europe) that likely acted as steppingstones in the global spread of the German cockroach. To examine the nature of population admixture during this spread, we performed allele-frequency-based tree reconstruction as implemented in TREEMIX v.1.13 (11). The tree of population divergence produced by TREEMIX was consistent with our ancestry estimation and spread route reconstruction (Fig. 1*D*).

We found the ancestor of the German cockroach to be the Asian cockroach, probably living in human settlements, with two domesticated lineages (agricultural/peridomestic and building environments), around 2,100 years ago (ya) when human civilizations were thriving in South Asia. We determined that the global spread of German cockroaches was initiated along two routes, west and east of the origin in India or Myanmar (Fig. 1*C*). As German cockroaches were known to hitchhike in soldiers' bread baskets (12), the expansion (~1.2 kya) westward was probably due to intensifying commercial and military activities of the Islamic Umayyad or Abbasid Caliphates. The expansion (~390 ya) eastward was likely facilitated by European colonial commercial activities between South and Southeast Asia (perhaps the Dutch and British East India Companies).

As recently as the 18th century, the German cockroach was still mostly contained within Asia. Our estimated time for their entry into Europe (~270 ya) matches the earliest historical records in the 1760s (6). The German cockroach then spread to the rest of the world between the late 19th and early 20th century, consistent with the highest volume of first records (6). Advances that accelerated transportation (e.g. steam engines) and thus globalization of trade, and increased comfort in housing (plumbing and indoor heating), allowed German cockroach populations to colonize regions that had been previously inaccessible due to high mortality during long-distance travel and poor cold tolerance (6).

We identified six migratory events in the TREEMIX results, most of them at locations where human commercial activities would lead to an overlap of cockroaches from different ancestries. For example, the population in Singapore was introduced through the West route but received substantial migration from neighboring Indonesian populations (Fig. 1*D*). As admixture during biological invasions may facilitate adaptation to new environments (13), future studies could focus on the functional genomic aspects of this admixture to understand German cockroaches' rapid spread, evolution of insecticide resistance, and so inform better integrated pest management (5, 6).

Materials and Methods

We collected 281 German cockroach samples from 57 sites in 17 countries across all human-inhabited continents. To acquire the COI gene, we sequenced mitochondrial genomes for 53 individuals, one individual per site, following published protocols (14). To acquire genome-wide SNPs, we followed published double digest restriction-site associated DNA library preparation protocols and associated bioinformatic pipelines (15). The COI dataset with 53 samples of the German cockroach and three samples of other *Blattella* species was used to create the haplotype network, whereas the SNP dataset of 281 samples was used to investigate population genetic structure and reconstruct the global spread of the German cockroach. For a detailed description of analyses, please see *SI Appendix*.

Data, Materials, and Software Availability. Raw sequence data for COI (NCBI accession PP692240–PP692292) (16) and genome-wide SNPs (PRJNA1099617) (17) are publicly available in NCBI. Tissue and DNA samples are stored in the Department of Entomology at Texas A&M University, USA. Materials are available upon request. Codes and scripts used for analyses are available at: https://github.com/qt37t247/German_cockroach_ddRAD (18).

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