The Evolution of Suidae

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Abstract
The Suidae are a family of Cetartiodactyla composed of 17 species classified in a minimum of five extant genera that originated at least 20 million years ago. Their success is evident in the multitude of habitats in which they are found as both natural and feral populations in tropical Island Southeast Asia, the high plateau of the Himalayas, Siberia, North Africa, the Pacific Islands, Australia, and the Americas. Morphological and molecular analyses of these species have revealed numerous aspects of their biology, including the ease with which many lineages have and continue to hybridize. This trait has made them an ideal model for evolutionary biologists. Suid species have also shared a deep history with humans, from their association with early hominids in Africa to their domestication. Here we review the current knowledge of this fascinating group and provide a comprehensive evolutionary history from the Oligocene to the present day.
INTRODUCTION

The Suidae are a widespread family of Cetartiodactyla that originated in the Oligocene at least 20 million years ago (Ma). They last shared a common ancestor with the Tayassuidae (New World Suidae) during the late Eocene/early Oligocene. The Suidae family has been extremely successful, having colonized the African and Eurasian continents. Given the diversity of fossil Suidae in Eurasia and Africa, they have been used as a stratigraphic dating tool for decades. This diversity is still apparent today, and the family is composed of a minimum of five extant genera made up of 17 species in Africa and Eurasia. The success of these species is evident in the multitude of habitats in which they are found, including tropical Island Southeast Asia (ISEA); the high plateau of the Himalayas; and the diverse environments of Siberia, central and western Eurasia, and North Africa.

Morphological and molecular analyses of these species have revealed numerous aspects of their biology, including both their speciation and the ease with which many lineages have and continue to hybridize. This trait has made them an ideal model for evolutionary biologists, though it has also complicated the identification of taxonomic species. Lastly, suid species have had a long shared history with humans, from their association with early hominids in Africa, to their domestication (that today makes them a prime source of protein for billions of people), to their modern use as a biomedical model. Here we review the current knowledge of this fascinating group of organisms and provide a comprehensive evolutionary history, from the Oligocene to the present day.

THE NATURAL HISTORY OF SUIDAE

Paleontological Perspectives

Suidae (also known as Suina or Suiformes) is a superfamily of even-toed ungulates (Cetartiodactyla). Suidae comprises many extant and extinct taxa of pig-like families, such as Tayassuidae in the Americas (tayassuids, peccaries, or javelinas) and Suidae (also known as suids, hogs, or pigs) in Eurasia (Figure 1). For decades the Suidae were grouped together with Hippopotamidae (hippos) until molecular analyses (1) demonstrated that the latter are instead more closely related to Cetacea (whales). Taxonomic relationships within Suoidae have typically been assessed based on morphological characters (e.g., Reference 2, 3), though molecular studies focusing on few nuclear and mitochondrial genes (4, 5) have also been employed. Both of these approaches have limitations, and our understanding of the early evolution of the superfamily remains limited. The New World (Tayassuidae) and Old World suids (i.e., Suidae; Figure 1) diverged during the late Eocene or the early Oligocene (~34.50–39.69 Ma based on molecular estimates) (5) (Figure 1). In addition, morphological analyses of fossils have inconclusively classified multiple Eocene fossils from Eurasia (Palaeochoeridae fossils such as Dolichochoerus and Palaeochoerus; Figure 1) and North America (e.g., Perchoerus) as crown Tayassuidae or Suidae or as stem groups of Suoidae (e.g., Reference 2). Thus, the monophyly of New World Suidae remains uncertain, as does the possibility that suids colonized the Americas more than once. Future molecular work (allowing for discrimination between Eocene or Oligocene divergence) and morphological studies will surely shed light on the early evolutionary history of these species.

Poor fossil preservation and homoplasy have made it difficult to resolve the root of Suidae (2, 6–8), and the classification of the earliest suids dating to the Oligocene remains problematic. Given the presence of fossils found in Pakistan, however, Suidae likely had already radiated into multiple subfamilies during the Oligocene (9). The first unequivocal and widespread appearance of the Suidae family is found in early-Miocene deposits of Africa, Europe, and Asia (~20 Ma; 6, 10–12). By the middle Miocene (~15 Ma), this family had colonized continental Eurasia and Africa.
Figure 1
Phylogeny of extinct and extant Suinae. A phylogeny of extinct and extant suid species built from molecular (5, 29) and morphological (2) studies. The † symbol represents extinct families or species. The age of each node is approximate and compiled from multiple sources of evidence. The colors of the branches represent the indigenous geographical regions of each extant species: Island Southeast Asia (dark blue), mainland Asia (light blue), Europe (orange), and Old World (green). Red dots indicate nodes that are supported using molecular analyses.

Recent analyses of fossil material recognized at least four subfamilies of Suinae from the Miocene: Listriodontinae, Cainochoerinae, Hyotheriinae, and Tetraconodontinae (2) (Figure 1). These Miocene subfamilies possessed a great deal of morphological diversity, likely as a result of the expansive geographical range they occupied (2, 13, 14). The taxonomy of these species has been studied extensively, especially in Africa, given their usefulness as a bio-chronological marker and their common occurrence with early hominid fossils (i.e., 13, 15–17).

A new subfamily of Suinae, the Suinae, emerged in the fossil record in the late Miocene (>10 Ma) (Figure 1). The Suinae rapidly expanded and diversified into multiple tribes found...
Figure 2

The enigmatic 

Babyrousa. (a) Picture of a male babirusa. (b) The oldest known cave painting in the world, dated to ∼35 ky ago and found in Sulawesi, Indonesia, features a depiction of a Babyrousa (155).

in late-Miocene strata across Eurasia and Africa (18, 19). This subfamily’s success was such that by the end of the Miocene almost all other subfamilies of Suidae had disappeared from the fossil record (2, 20). Across Eurasia and Africa, the subfamilies of Suidae, including Listriodontinae (21), Cainochoerinae (22, 23), and Hyotheriinae (24), also went extinct before the Miocene/Pliocene boundary (Figure 1). Their disappearance may have allowed or even induced the diversification of Suinae in Africa, allowing for the emergence of the ancestors of extant sub-Saharan suids: the forest hogs (Hylochoerus), river hogs and bush pigs (Potamochoerus), and warthogs (Phacochoerus) (5, 13, 25–27). All of the subfamilies of non-Suinae also disappeared in Eurasia shortly after the Miocene/Pliocene boundary. This replacement gave rise to the ancestor of modern pigs (Sus) as well as a myriad of other, now extinct, tribes.

By the Pliocene/Pleistocene boundary, only two remaining subfamilies of Suidae were found across Eurasia: the Suinae (including extant suids) and the Tetraconodontinae [including the genera Nyanzachoerus in Africa (28) and Conohyus in Europe and South Asia (12)]. Although it is generally accepted that only Suinae survived to the present, the species of Babyrousa are a probable exception (Figure 2). These species have been classified as both Suinae and Babyrousinae, and recent molecular clock analyses reported that they diverged from the extant Suinae during the middle Miocene, around 13 Ma (18–9 Ma; 5), approximately 3 My before African and Eurasian Suinae diverged from a common ancestor (14–7 Ma) (5, 29). Thus, although the inclusion of Babyrousa within Suinae or in its own subfamily is primarily a nomenclatural issue, this debate highlights the enigmatic nature of this genus (see sidebar, The Enigmatic Babyrousa).

Many other tribes of Suinae thrived during the Pliocene. For instance, Asian taxa included the Porcula, Sus, and endemic Sulawesi genus Celebochoerus (30). The genus Porcula is currently found only in a small pocket of sub-Himalayan grasslands in Northeast India, though it occurred much more widely (on the island of Java and in eastern China and Burma (31)) in the Pleistocene.
THE ENIGMATIC BABYROUSA

The enigmatic Sulawesi babirusa (*Babyrousa*) (meaning “pig deer” in Indonesian) is a charismatic and wrinkle-skinned species. Male *Babyrousa* have characteristic long, thick, and often rotating upper canines (Figure 2). Little is known about the evolutionary history of this peculiar species, mainly because of a complete lack of extinct or extant closely related species. *Babyrousa* is anatomically distinct from other Suidae (156–159) and is restricted to remote areas of Island Southeast Asia (i.e., Sulawesi, Buru and the the Togean Islands, Masbate, Taliabu, and Samana). Thus, this enigmatic species could be considered a relic of the once diverse but now extinct Miocene Suidae. In 2006, despite significant karyotypic differences, an unexpectedly successful hybridization between a male *Babyrousa* and *Sus scrofa* took place at Copenhagen Zoo (154). The mating produced five offspring, three of which lived for months before being culled. Lastly, although never domesticated, *Babyrousa* have interacted with humans for millennia, as highlighted by one of the earliest cave paintings clearly picturing a *Babyrousa* female (Figure 2). Babirusas are listed as vulnerable or endangered (depending on the species) by the International Union for Conservation of Nature Red List as a result of deforestation and hunting pressure for meat or Balinese ceremonial masks (160; A McDonald, personal communication).

There is a great deal of debate surrounding the chronology and geographic origins of the earliest *Sus* fossils (i.e., 31, 32). For instance, though claims for the earliest *Sus* fossils are dated to the late Miocene or early Pliocene in Europe, paleontologists and geneticists alike have argued for an East Asian origin of the genus (20, 29). In addition, the genus may well have originated much later during the Pliocene (Figure 1). What is not controversial is that by the late Pliocene, this genus had colonized most of continental Eurasia and ISEA, effectively replacing all other Suinae genera besides the sub-Saharan Suinae and *Babyrousa*.

The genus *Sus* then diversified into multiple species. Though many remain extant, all but one (*Sus scrofa*) are restricted to ISEA, including *Sus barbatus* (Borneo, Sumatra, and Malay Peninsula), *Sus verrucosus* (Java and Bawean), *Sus celebensis*, *Sus oliveri*, *Sus ahoenobarbus*, *Sus philippensis* (the Philippines), and *Sus celebensis* (Sulawesi). Several *Sus* species once existed on continental Eurasia, including *Sus minor* from Europe and China (33), *Sus strozzi* from Europe (34–36), and *Sus peii/Sus xiaozhu* from China (37), but they disappeared following the spread *S. scrofa* (the ancestor of domestic pigs) from Southeast Asia (34, 35).

Genomics Perspectives

Of the three major episodes of species replacement that took place during the evolutionary history of Suidae, including (a) the disappearance of most non-Suinae (except *Babyrousa*) during the Miocene/Pliocene boundary, (b) the replacement of all non-*Sus* species in Eurasia during the Pliocene, and (c) the replacement of most *Sus* species by *S. scrofa* during the Pleistocene, the latter is the best documented. Over the course of 1–2 My, *S. scrofa* colonized the entirety of Eurasia and North Africa and replaced many local species. This large-scale expansion left traces in the genomes of contemporary *S. scrofa* populations, including evidence of a large increase in its effective population size (N_e) before a demographic reduction that occurred during the last glacial maximum (38, 39). *S. scrofa* adapted to a myriad of new environments over a relatively short evolutionary timescale. Although they originated in the tropical forests of mainland Southeast Asia (29), these suids adapted to life in the high-altitude Himalayas (40), the northern latitudes of Eurasia (41), warm climates in the Near East and North Africa, and temperate climates in mainland Europe (38).
Selective sweeps resulting from adaptations to novel habitats during this large-scale expansion are also evident in the genomes of *S. scrofa* (38, 40, 41). Regulatory mechanisms (microRNAs) and olfactory receptors (ORs) were most affected by natural selection (38, 42). ORs are encoded by small open reading frames (lacking introns) that are expressed in the brain and airways. The products of these genes provide the basics of the smell machinery by binding to specific odor molecules and producing a nerve impulse transmitted to the brain. The swine genome-sequencing consortium reported that pigs carry over 1,301 OR genes (38) and over 1,113 functional ORs (non-pseudo genes; 43). This number of functional OR is approximately equivalent to the number found in rats (1,201 ORs) and is more than that of any other mammal sequenced to date [mouse = 908, dogs = 872, humans = 457 (43)]. Moreover, the rate of pseudogenization (loss of function) at OR is lower in pigs than in any other mammalian species (~13%; 43). The prominence of OR in the genome of suids highlights their strong reliance on smell for foraging or mate recognition.

Interestingly, ORs are often highly variable in copy number (number of copies of genic or nongenic region) not only in pigs but in many vertebrate species (44–48). Gains and losses of OR are exacerbated in the pig genome, resulting in major copy number variations (CNV) between populations, often ranging from 1 to 40 or more copies in various populations across Eurasia (Figure 3) (42, 49). Although OR are clearly the most CNV-prone genes in the pig genome, other genes are also affected by these duplications/deletions that accumulate at a much higher rate than single-nucleotide polymorphisms (SNPs) (1.4 times higher) (44, 49). The great evolutionary potential of CNV at OR could have provided *S. scrofa* with the necessary plasticity to evolve new foraging strategies, allowing them to rapidly adapt to novel environments. Interestingly, CNV at ORs also may have played a prominent role in the maintenance of reproductive isolation during the speciation of *Sus* species in ISEA, further supporting the importance of olfactory genes during the evolutionary history of suids (49).

**Resolving Taxonomic Conflicts in the Era of Genomics**

Genomic sequences are a powerful tool not only to investigate the effects of natural selection but also to resolve conflicting taxonomic and phylogeographic perspectives of evolutionary history. In addition, genomes can also provide insights into the mechanisms underlying these conflicts. The evolutionary history of Suidae has been particularly complex (and thus controversial), though genomic sequences from multiple species are now resolving these conundrums.

In 2005, Larson et al. (50) published a worldwide phylogeographic analysis of *Sus* species based on mitochondrial DNA (mtDNA). This study demonstrated that multiple populations of *S. scrofa* across Eurasia were both geographically and genetically differentiated. Despite being morphologically well defined, however, species in ISEA lacked any mitochondrial distinctiveness (Figure 1) (50, 51). This paradox was deepened by the lack of agreement between multiple phylogenetic studies based on mtDNA (4, 52), and the lack of mitochondrial differentiation between morphologically divergent species remained puzzling.

The advent of genome sequencing provided the necessary power to resolve this paradox (29, 53). These studies demonstrated that mitochondrial genomes among ISEA *Sus* species had been acquired during hybridization episodes and therefore no longer reflected species divergence patterns (Figure 4). Although the nuclear genomes of these species had also been affected by hybridization, they possessed sufficient resolving power to generate a robust phylogenetic reconstruction and to obtain reliable divergence time estimates of the species (29).

Controversy has surrounded the taxonomy of the sub-Saharan suids as well. Although recent analyses of nuclear and mitochondrial markers have apparently resolved the debate (5), multiple
Figure 3
Heat map picturing the high copy number variability for 100 olfactory receptor genes in multiple pig genomes. Rows represent different pig populations. Each column represents a single olfactory receptor. Colors correspond to the number of copies of each gene in different populations. The raw data were obtained from Reference 42. Abbreviations: AsD, Asian domestic; AsWB, Asian wild boars; EuD, European domestic; EuWB, European wild boars.

studies of fossil remains yielded contradictory results (13, 15, 54–56). The emerging consilience now suggests that Suidae colonized Africa from Eurasia approximately six times (57), the most recent of which took place in the Miocene, based upon Suinae fossils found in the Chad deposits from the Miocene/Pliocene boundary (∼5.5 Ma; 25). What remained unclear was whether the major lineages of African Suinae evolved in Eurasia or Africa.

Gongora et al. (58) suggested that the direct ancestors of the major lineages of African Suinae might have diverged outside of Africa because their divergence times (7–14 Ma) significantly
Figure 4
Conflicting taxonomy across the genome of Sus species—evidence for reticulation in Asian pigs. (a) Map depicting the range of multiple Sus species in mainland and Island Southeast Asia. Light gray area represents the contour of Sundaland, a large continental shelf with shallow seas that would have been exposed during glacial periods. (b) Genome-wide phylogeny of Sus species from Reference 78. (c) Mitochondrial phylogeny of Sus from Reference 29 showing all Sundaland species grouping together owing to admixture during glacial periods. (d) A phylogeny inferred from a small proportion of chromosome X, adapted from Reference 41, showing how North Eurasian and South Eurasian populations cluster, most likely as a result of admixture with a now-extinct species in northern China. (e) A diagram depicting known occurrences of hybridization between Suidae species as inferred from genome sequence (29, 41, 154).
predated those of the earliest Suinae fossil in Africa (5.5 Ma). However, the current fossil evidence of Potamachorhus-like fossils found in Eurasia is from the Early Pliocene strata (59, 60). The presence of these fossils may have resulted from the migration back out of Africa by Potamachorhus during the Pliocene. In addition, and in direct opposition to the data from molecular phylogenies (5), paleontologists have argued that African Suinae may in fact be paraphyletic, and that the African lineages are the result of at least two waves of colonization (13, 57).

These conflicting views stem from peculiar and seemingly homologous morphological characteristics among warty pigs found in Eurasia and Africa. The idea of a single warty pigs genus, Dasychoerus, goes back to Gray (61) and was recently resurrected by multiple authors (i.e., 13, 31, 32, 57). Dasychoerus includes multiple species, such as the Java warty pig S. verrucosus, the Sulawesi warty pig S. celebensis, and the giant forest hog Hylochoerus meinertzhageni (13). This perspective contradicts recent molecular phylogenies (5, 29). If the molecular sequences are correct, then the lack of monophyly among species in the Dasychoerus genus and the shared morphological features [i.e., facial warts and dental similarities (13)] must be a result of convergent evolution.

**Hybridization and Taxonomic Conflicts**

The recent sequencing of multiple Sus genomes (29, 38) has provided novel insights into these paradoxes. The wealth of information afforded by genomes has allowed not only for a resolution of multiple, long-standing taxonomic issues (such as the Sus species in ISEA) but also for an in-depth investigation of the underlying mechanisms behind these paradoxes (29, 38, 41). It is now evident that a bifurcating classification (such as a classic phylogenetic tree, as in Figure 1) for Suidae does not provide a comprehensive approximation of their true evolutionary history. Instead, genome sequences have demonstrated that the evolutionary history of Sus is best explained by a reticulate history resulting from many episodes of interspecific admixture (Figure 4).

One clear example of the power of genomes to resolve paradoxes in Suidae is the discovery of recent interspecific admixture events between Sus species that resulted in the apparent lack of taxonomic information in their mtDNA (29). These interspecific admixture episodes were most likely induced by land bridges that appeared between the islands of Borneo, Java, and Sumatra during the glacial periods of the Plio-Pleistocene (62) (Figure 4a). Interestingly, these introgressions were markedly asymmetrical (53), as demonstrated by the fact that whereas ∼23% of the genome of S. scrofa populations from ISEA was acquired from the endemic Javan warty pig (S. verrucosus), only ∼5% of the genome of S. verrucosus was the result of admixture with S. scrofa (53). It is also possible that this asymmetry from an endemic species (S. verrucosus) into an “invasive” species (S. scrofa) (29) could have been adaptive.

The same admixture scenario likely also took place as S. scrofa expanded within China, as revealed by the discovery of peculiar divergence patterns and unexpected genealogies on the X chromosome of S. scrofa populations from southern and northern China (41). The genomic region in question spans multiple megabase pairs and displays extreme nucleotide divergence between northern and southern Chinese populations of S. scrofa compared with the rest of the genome (29, 38). The divergence in this region is such that southern Chinese S. scrofa cluster with the Sus species from ISEA, whereas northern Chinese S. scrofa cluster with European populations (Figure 4d). This region on the X chromosome may also be linked to adaptation to high latitude (41). One explanation for this phylogenic pattern is that it resulted from interbreeding between S. scrofa and an extinct species as the former reached northern China (41). The newly acquired haplotypes swept to fixation owing to the advantage they provided in northern latitudes and were transmitted to European populations during migrations across Eurasia (41).
Conclusions

Fossils provide a fundamental source of information that allows for the establishment of new hypotheses regarding the complex evolutionary history of Sus. These can now be tested using whole-genome sequencing. Combining information from molecules and fossils, researchers have demonstrated that although morphological homoplasy may play a role in resolving conflicting phylogenies (2), the lesson from genomic signatures is that interspecific admixture was common during the evolution of suids and has led to mixed evolutionary legacies. For example, genome sequences have demonstrated that S. scrofa did not simply replace other species, but often admixed with them prior to their extinction. This scenario has been demonstrated recently in other species, including humans, who hybridized with other hominins prior to their extinction (63, 64).

Admixture may therefore explain unresolved taxonomic questions (e.g., warty pigs). Hybridization may also have provided pigs with the means to rapidly adapt to new environments by borrowing genetic material, such as OR repertoires, from local, yet closely related species. This mechanism also appears to be true of humans who were able to survive in high altitudes in Tibet thanks to admixture with Denisovans (65). This phenomenon provides a testable hypothesis to explain how suids extended their range and adapted to novel environments on numerous occasions during their expansion. The advent of genomic studies, informed by paleontological evidence, will shed light on the potential of hybridization as an adaptive mechanism in suids. Lastly, it is now clear that the complicated evolutionary history of Suidae, involving numerous adaptations, turnovers, and reticulations, makes this family a great model for the study of speciation and adaptation.

THE ARTIFICIAL HISTORY OF SUIDAE

A detailed evolutionary history of Suidae would be incomplete without a discussion of the shared history between humans and pigs. From early translocation by modern hunter-gatherers to intensive breeding by modern farmers, suids and humans have interacted for millennia, and their common artificial history mirrors the complexity of the natural history of Suidae.

Worldwide Translocation of Wild and Domestic Pig

Over thousands of years, humans have not only domesticated pigs but also translocated suid species across the world as domestic and wild stock (Figure 4). In Africa, humans most likely transported bush pigs (Potamochoerus larvatus) from the continent to Mayotte, Comoros, and Madagascar (Figure 2), though the chronology of this movement remains uncertain (66, 67). In ISEA, three presumed translocations of suids stand out for their conservation importance: (a) the suspected but as yet unproven introduction of Babyrousa to the Sula and Buru Islands; (b) the introduction of S. celebensis to Simeulue Island, northwest of Sumatra, and to the Moluccas and Lesser Sundas (68, 69); and (c) the introduction of S. scrofa as a domestic animal to the Andaman and Nicobar Islands, eastern Indonesia, and New Guinea (51).

The translocation of S. celebensis from Sulawesi throughout ISEA, including the Lesser Sunda Islands, such as Flores and Timor, and possibly as far west as Bali, has been established on morphological and genetic evidence (Figure 2) (51, 69, 70). The genetic ancestry of pigs found east of Java (Sus heareni), however, remains unresolved, and they may be hybrids between introduced S. celebensis and S. scrofa brought by dispersing modern humans. S. celebensis was also possibly introduced to Simeulue (71). Although genomic analyses may support this claim (29), how these pigs were transported across the 3,500-km sea voyage from Sulawesi to the west of Sumatra remains unsolved, because there is no archaeological evidence to track the route or date the arrival of these
To Polynesia including Hawaii and New Zealand

Figure 5

A map of Eurasia depicting the human-mediated translocation of wild and domestic suids across the world prior to the fifteenth century AD, when European explorers introduced pigs to the Americas. Green squares indicate indigenous populations of wild suid species that were transported by people along the routes indicated by the green arrows. The question mark in Africa alludes to the fact that the source population of Potamochoerus larvatus transported to Madagascar is unknown. The inset shows the transport of wild boar (from either Anatolia or the Levant) to Cyprus prior to the advent of domestication (72). Yellow circles depict the locations where East Asian and Anatolian populations of wild boar were independently domesticated and then transported away from the domestication centers along the black arrows. Red circles indicate the regions where genetically and geographically distinct populations of wild boar hybridized with domestic pigs, often leading to the acquisition of mitochondrial and nuclear DNA from local wild boar into domestic stocks.

Not surprisingly, domestic pigs were subjected to human-mediated transport throughout Eurasia and Oceania during prehistory (Figure 5). Pigs also accompanied explorers beginning in the ninth century, when they were introduced to Iceland (73) and Greenland (74), and from the fifteenth century onward to the American continents (75), New Zealand, and Australia. Many of these introduced individuals from various genetic origins (76) were deliberately released or escaped, thus giving rise to feral and invasive populations, and they now pose threats to local biodiversity worldwide (77). The impact of European domestic pigs can also be seen in Indonesia and the Philippines, where they have hybridized with local species (78).

Pig Domestication

Though numerous species have been domesticated, the vast majority have entered this relationship in the past 500 years (79). Pigs were among the first animals, along with goats, sheep, and cows, to be domesticated at the beginning of the Holocene as part of a move toward sedentary societies.
Our understanding of the process, timing, and number of independent domestication episodes has advanced considerably as new evidence and perspectives have recently been published on theoretical, archaeological, and genetic fronts.

From a more general perspective, there are several morphological and behavioral similarities between domesticated versions of animals whose ancestors are not closely related. A common historical interpretation of this pattern has posited not only that the process of domestication was the same for all species but that human intentionality played a significant role. Both Vigne (80) and Zeder (81) have recently challenged this convention and proposed instead multistage processes that do not (at least initially) require deliberate human forethought. In Vigne’s view, early animal domestication proceeded from anthropophily, to commensalism, to control in the wild, to control of captive animals, to extensive breeding, to intensive breeding, and finally to pets. Although this was certainly true for some animals, Zeder further recognized and described three separate pathways—commensal, prey, and directed—that animals followed into a domesticated relationship with humans.

Crucially, the commensal pathway does not begin with intentional action on the part of people to domesticate animals. Instead, populations of some wild animals would have been attracted to elements of the human niche, including human food waste and other smaller animals. Within the context of Zeder’s and Vigne’s models, the initial attraction of animals following the commensal route could have progressed through various stages of intensifying relationships and human control until people were responsible for breeding in captivity. In a recent study of global patterns of animal domestication, Larson & Fuller (79) demonstrated that animals following the commensal pathway (such as dogs) always preceded those that entered into domestication along other trajectories.

Prey pathway taxa are generally associated with settled human communities. Zooarchaeological assemblages document changes in the management strategies of hunted sheep, goats, pigs, and cows in the Fertile Crescent starting approximately 11,700 years ago. A recent study of animal remains at Sha’ar Hagolan, Israel, demonstrated that cows and pigs were overhunted prior to domestication (82), suggesting that intensive exploitation forced humans to adapt their management strategies, after which the animals gradually became domesticated following the prey pathway. This pattern of overhunting prior to domestication suggests that the prey pathway was as unintentional as the commensal pathway (83).

Of the three, only the directed pathway begins with a deliberate human objective to domesticate a species (81). Before these species were domesticated, humans were already reliant upon a wide range of domestic plants and animals. Even in the cases of horses, donkeys, and Old World camels, however, domestication was a multigenerational adaptation to human selection pressures, including tameness, herding behavior, and the ability to breed in captivity. The reason the existence of different pathways took so long to be recognized is likely because the majority of modern domestic animals have arisen only in the past few hundred years, including many small animal pets and an increasing number of aquatic species (84), and they have virtually all followed the directed pathway.

The specific descriptions of the different trajectories animals followed are useful but not mutually exclusive. Pigs, for example, may have been domesticated as populations became accustomed to the human niche, which would suggest a commensal mode, or they may have been hunted and followed a prey pathway, or perhaps both. What is clear is that pigs were definitively domesticated in at least two locations: East Asia and the Near East.

Zooarchaeological records demonstrate clearly that pig domestication took place independently in the Near East, as revealed by demographic changes in Sus remains excavated from archaeological sites in Eastern Anatolia, including Çayönü Tepesi, Hallan Çemi Tepesi, Hayaz Tepe, Tell Hallula, and Gürcütepe. For instance, the site of Çayönü Tepesi possesses a unique
stratigraphic sequence spanning 12,000 to 8,300 years ago (85, 86), demonstrating that pigs were killed at progressively younger ages, suggesting an intensification of human-mediated selection consistent with the onset of domestication. Additional changes associated with intensifying domestication, including snout shortening and hypoplastic defects in the dental enamel [as a result of physiological stress (85, 87)], are also visible. This intensification occurred gradually over the duration of the sequence, and the pigs did not appear domesticated according to modern morphological criteria until 8,300 years ago (85).

Excavations at the early Neolithic Turkish site of Hallan Çemi Tepesi (also in the eastern Taurus Mountains) have suggested that a shift away from wild behavior may have taken place even earlier than at Çayönü. In a review of Sus data from several sites, Peters et al. (88) observed a decrease in the length of the third molar over time, which they said provided “unequivocal morphometrical evidence for the occurrence of domestic pigs” in the Late Pre-Pottery Neolithic B phase (89). In addition, Peters et al. (88) highlighted data from other sites, including Hayaz Tepe and Tell Hallula, to substantiate their claim for the early appearance of domestic pigs. Regardless of the exact timing, it is apparent from the zooarchaeological evidence that wild boar adapted to human settlements in Eastern Turkey, and that this process resulted in the domestic pigs we recognize today.

Outside of the Near East, China is the only other location where clear archaeological evidence has been presented in support of independent pig domestication. Large-scale excavations have revealed that agricultural activities were practiced by seasonally mobile cultivators along the Yellow River ∼8,000 BP (90–92), and plant cultivation may have begun 2,000 years earlier in the Yellow River Valley (93). In southern China, sedentary hunter-gatherers (94) began cultivating rice along the Yangtze River approximately 9,000–8,000 BP, a practice that eventually culminated in the dependence upon rice agriculture by ∼6,000 BP (91). Archaeological evidence suggests that though domestic pigs made up only a small percentage of the earliest mammal bone assemblages, they were prevalent in both northern and southern China by at least 8,000 BP (95, 96).

Claims for the much earlier appearance of domestic pigs (∼12,500 years BP) at the site of Zengpiyan near Guilin were refuted by a reanalysis of the zooarchaeological record that also demonstrated a clear long-term shift toward domestication at the site of Jiahu (97). A revised analysis of previously excavated Chinese assemblages, along with the discovery of new sites, has led to a refined model of pig domestication in China along a long stretch of the Yellow River and on the Lower Yangtze River ∼8,000 years ago (98). The geographic scale of China, where at least two subspecies of wild boar exist, also possesses a substantial diversity of Neolithic cultural entities scattered across a mosaic environment (56, 99, 100). Rather than a single geographical setting, these data suggest that, like in Eastern Turkey, pig domestication may have taken place across a diffuse, regional scale.

The first results of a genetic analysis of domestication focused on patterns of mitochondrial variation in domestic pig and wild boar samples from across the Old World. The initial results demonstrated that domestic pigs from East Asia and Western Europe shared closer affinity to wild boar from those regions than to each other, thus confirming the hypothesis that pigs had been domesticated at least twice from geographically and genetically differentiated populations of wild boar (101). Numerous subsequent studies using mitochondrial (50, 102, 103) and nuclear markers, including microsatellites (104, 105), SNPs (106), and whole genomes (29, 38, 41), have confirmed the unique genetic identities of East Asian and European wild boar, as well as the significant genetic differences between domestic pigs on either side of the Old World.

Most of these studies have not sampled wild boar from across its natural range. An early mitochondrial study (50) that did so, however, revealed not only that wild boar retained a strong phylogeographic signal but also that many domestic pigs possessed mitochondrial signatures that clustered in clades consisting of wild boar from Europe and Asia (as expected), as well as Italy,
India, and peninsular Southeast Asia. This result led the authors to speculate that wild boar from numerous regions may have been domesticated independently.

If this is true, and if pigs followed the same pathway to domestication in many different geographical settings, then the long-term demographic and morphological changes found in pigs recovered from archaeological sites in Eastern Turkey and China should also be visible in the zooarchaeological records of Western Europe, India, and peninsular Southeast Asia. In fact, they are not. Domestic pigs appear suddenly alongside wild boar in Europe and in peninsular East Asia, where they are associated with incoming farmers. This archaeological observation has been substantiated by ancient DNA studies of pigs in Anatolia and Europe, demonstrating that the earliest domestic pigs in Europe possessed mitochondrial haplotypes found only in Anatolia and the Near East (107, 108).

In East Asia there is a similar lack of consistency between the genetic and archaeological records. Though ancient DNA signatures from several sites in China match those of modern Chinese domestic pigs (109), domestic pigs associated with the Austronesian expansion into the Pacific possessed signatures found in wild boar indigenous to peninsular Southeast Asia (51). As they do in Western Europe, domestic pigs appear suddenly alongside wild boar (109), and no archaeological evidence supports a long-term domestication process in Southeast Asia.

The genetic evidence suggesting widespread and even common domestication of distinct wild boar populations seems to contradict the archaeological evidence that points toward only two centers of domestication in East Asia and the Near East. A survey of the domestication literature, however, demonstrated that far from being unusual, introgression between indigenous wild populations and translocated domestic populations domesticated elsewhere is common in both plants and animals (110). This admixture often results in an imported domestic population taking on the genetic [and morphological (111)] appearance of the local wild population, leading researchers to the false conclusion that the local wild population gave rise to the domestic one through an independent domestication process. In fact, this process is so pervasive that Larson & Fuller (79) have suggested the word domestication be reserved only for the independent process (regardless of pathway), and they introduce the term “introgressive capture” to refer to subsequent admixture between introduced domestic populations and local wild populations that were never domesticated.

Combining the evidence from archaeological and genetic perspectives yields two important insights. Firstly, despite the presence of geographically and genetically distinct wild boar populations across the Old World, the independent, long-term process of pig domestication took place in only two regions: Eastern Anatolia and China. Secondly, following these independent processes, domestic pigs accompanied farmers as they dispersed beyond the domestication regions. Once there, domestic pigs acquired mitochondrial and nuclear affinities through hybridization with the local wild boar. The result of this repeated admixture is that domestic pigs in Europe no longer possess an obvious genetic legacy of their Near Eastern heritage (107, 108, 112), and pigs native to Polynesia carry a mitochondrial signature that is not evident in any modern wild boar in central or northern China (109).

Hybridization between distinct domestication populations has continued, as exemplified by the development of improved breeds (hybrids between Chinese and European pigs) in the nineteenth century (113), and evidenced by the fact that 30% of the genomes of European commercial pigs are derived from East Asian breeds (114, 115). More generally, hybridization is emerging as a common feature in the natural and artificial history of suids. Unraveling the spatial and temporal histories of the appearance and spread of specific traits, as well as the overall pattern of admixture that may have allowed for the proliferation of pigs in new environments or selection regimes, will require both substantial ancient genomic DNA and sophisticated bioinformatic approaches. This
approach is tractable, however, and we may soon arrive at a satisfying history of pig domestication and dispersal, as well as shed light on the similarities between domestication and speciation.

THREATS TO NATURAL POPULATIONS

Asian Suidae

Apart from the near ubiquitous S. scrofa, all other wild pig species in Asia are listed on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (116) as Near Threatened, Vulnerable (VU), Endangered (EN), or Critically Endangered (CR). All African pig species are of lower conservation concern, though taxonomic revisions within the morphologically and genetically highly variable forest hog (H. meinertzhageni) could result in much smaller ranges and higher extinction threat to, for example, the northern forest hog H. meinertzhageni in Ethiopia and southern Sudan.

One of the reasons for the different extinction threat levels in Africa and Asia could be the role that S. scrofa likely played in the extinction or near extinction of other pig species. S. scrofa occurs throughout mainland Eurasia and many parts of ISEA but only marginally in North Africa. All of Southeast Asia’s most threatened pig species, the Visayan warty pig S. celebensis (CR), Javan warty pig S. oliveri (EN), and S. barbatus, S. aboebobarius, and S. philippensis (all VU) are endemic to one or a few islands on the southeastern periphery of the Asian landmass. This raises the question of whether in most of mainland Asia the ecologically versatile S. scrofa displaced other pig taxa [such as S. (D.) stroazzi, see above] during the Pleistocene, leaving only the surviving island species.

During the Middle Pleistocene, pig diversity in mainland Asia remained high, as evidenced by the presence of seven or eight (chrono)species at the Liucheng site in China (31, 117). The distribution of the genus Porcula, which now occurs only in pockets of grassland habitat in India, was also much greater during the Pleistocene and may have been reduced by the expansion of S. scrofa. All pig species are threatened by anthropogenic factors, such as overhunting and degradation of natural habitats. In conservation terms, however, it is important to know whether species were already on a long decline because of the influence of a nonhuman species such as S. scrofa, and whether modern humans are only providing a final push toward extinction.

An example of this is the Indonesian island of Java, where the endemic S. verrucosus has co-occurred with S. scrofa since the Late Pleistocene or early Holocene (118). Until historic times, the two species lived side by side with limited ecological separation (119). More recently, S. verrucosus has declined rapidly and now survives only in small parts of its former range (120). The two species (S. scrofa and S. verrucosus) are known to hybridize in the wild, and it appears that the more rapidly reproducing S. scrofa is both outcompeting S. verrucosus and absorbing the species into its gene pool. A population of a related taxon, Sus verrucosus bluchi, on the small island of Bawean in the Java Sea has survived as a small population of approximately 350 animals for many centuries, possibly because S. scrofa is not present on the island (121).

This competition and hybridization model is hypothetical, but similar dynamics may have played a role in the apparent demise of another species. Despite a great deal survey work, Sus bucculentus, an endemic species of the Annamite Range in Laos, has not been found in recent times. The three known skulls of this species morphologically resembled S. verrucosus (122), although phylogenetic analysis of 12S and cytochrome regions of mtDNA of an alleged S. bucculentus specimen grouped it with a clade of S. scrofa (123). Full genome sequencing is needed to reveal whether S. bucculentus retains any S. verrucosus–like characteristics. If so, it may have been displaced by S. scrofa (or hunted out) and should be considered either extinct or an invalid species.
In general, there is limited knowledge of the in situ conservation status of most threatened pig species. The babirusa species of the Togean, Buru, and Sula Islands (Babyrousa togeanensis and Babyrousa babirussa) remain unstudied, and almost nothing is known regarding S. oliveri (124), which has never been photographed. In addition, population estimates and levels of hybridization with S. scrofa remain to be determined for the CR-listed S. cebifrons in the Philippines. Retaining viable populations of these ecologically important species is a high conservation priority (125, 126), despite the fact that they do not receive a great deal of international attention.

**Pygmy Hog (Porcula salvania)**

The pygmy hog (Porcula salvania) is the smallest and the most endangered of the world's wild suids. Historically it occurred in early successional tall grasslands along the southern Himalayan foothills (127), but it now appears to be extinct in Bhutan and Nepal and most of its Indian range, and it survives only in a few isolated grasslands areas in Assam (128). It is listed on the IUCN Red List of Threatened Species as CR, with loss and degradation of grassland habitat owing to human settlements, agricultural encroachments, dry-season burning, livestock grazing, commercial forestry, and flood control schemes being listed as the primary threats (129).

The recent discovery that the genus Porcula was actually widespread in South and Southeast Asia (31) during the Late Pleistocene and not restricted to a small sub-Himalayan habitat zone sheds a new light on what could be driving population declines in Porcula. Pygmy hogs are superbly adapted to life in tall grasslands. Their small size and bullet shape allow them to move through dense grasses, on which they also feed and which they use for building their sleeping and resting nests.

Presumably, Porcula used such grasslands throughout its range. Did all the Southeast and East Asian tall grasslands disappear at the end of the Pleistocene, leaving only the sub-Himalayan habitats, or did other factors play a role in the demise of Porcula? Is it possible that habitat alteration or predation by modern humans that arrived in the region some 60,000–100,000 years ago (130, 131) played a role? Or did S. scrofa, which dispersed into the region in the Middle Pleistocene, negatively impact Porcula? We currently do not have answers to these questions, but it is clear that placing the conservation of P. salvania within an evolutionary perspective more broadly informs our views on extinction threats. The ongoing pygmy hog genome-sequencing project will shed more light on the evolutionary history of this peculiar species and provide valuable insights for conservation (L. Frantz & M. Groenen, personal communication).

**Modern Wild Boar (Sus scrofa)**

Groves (56) placed all members of the S. scrofa group in a single species, but the differences between some of the taxa in the group are sharper and more consistent than previously recognized. Larson et al. (108), using the control region of mtDNA, found that this species group has a basal comb (which also included samples of S. celebensis), of which one branch contained all of the Eurasian samples. It appears that the ancestor of the S. scrofa group originated in Southeast Asia in the early Pleistocene, then spread to India in the mid-Pleistocene, and from there split into two European lineages and two eastern Asian lineages that separated approximately 600,000 years ago into a northern and southern group (29, 78, 132). Subsequent division occurred between Indian and Eurasian pigs, leading to a final distinctive clade of European and Middle Eastern samples (51, 78).

The genetic differentiation within S. scrofa is mirrored by significant morphological variation (56, 133, 134). Approximately 80 taxa have been described within what we now consider S. scrofa (135), from which 15 are recognized as subspecies (56). Groves & Grubb (136) proposed elevating
three of these to species level on the basis of consistent morphological differences: (1) *Sus moupinensis* (Milne-Edwards 1871) in Burma and China, (2) *Sus chirodontus* (Heude 1888) in south-central China, and (3) *Sus assericus* (Heude 1888) in Heilongjiang/the Far East; however, this proposal remains just that. Further molecular studies are required to assess whether the morphological differences between the three proposed species are reflected by similar genetic patterns.

Phylogenetic patterns within *S. scrofa* must be explored further. Clear morphological differences exist, for example, in the long-maned, thick-haired pigs of mainland India and further west, and those of northeastern India, Myanmar, and mainland Southeast Asia. The Japanese Ryukyu pig (*S. scrofa riukiuanus*) also possesses morphologically and genetically distinct characteristics (137–139), and the Indonesian, white-snouted, rough-haired pigs also stand out (56). The so-called Lanyu pigs, which are supposedly derived from the islet of Lanyu off the coast of Taiwan, possess a unique mitochondrial signature, suggesting a possible distinctive evolutionary history as well (140). Differentiation between all these taxa has likely been suppressed through introgression with other subspecies and domestic pigs. Indigenous wild boar pig populations are increasingly isolated from each other in Asia, and as long as they remain extant and avoid assimilation by domestic pigs, the differences between them may become more pronounced.

**MODERN BREEDING AND THREATS TO DOMESTIC POPULATIONS**

Threats to naturally occurring suids are not the sole conservation issue for Suidae. Thousands of years of introgression between wild boar and domestic pigs, as well as crossbreeding between domestic stocks, have resulted in a myriad of phenotypic differences between domestic pig populations. The establishment of pig breed societies and herdbooks did not occur until the Industrial Revolution in the eighteenth and nineteenth centuries, when British breeders started to import and crossbreed Asian and European pigs to meet the increasing demand for pork meat (115). China too had a long history of breeding, with countless distinct populations. Instead of herdbooks and types, Chinese pigs are often named after their geographic location of origin, most likely owing to the large cultural, climatic, and topographic variations found across the country.

Europe is not immune to complications resulting from attempting to define breeds, because many countries and breeding companies maintain different populations of the same breed with widely different genetic ancestry. This is illustrated by the Domestic Animal Diversity Information System hosted by the Food and Agriculture Organization of the United Nations (FAO) (http://dad.fao.org), which for pigs contains 1,286 different entries for breeds/lines across the world and 778 specific breeds. Pork is one of the most consumed protein sources worldwide, and approximately 115 million tons are produced globally every year (141), but only a handful of commercial breeds are responsible for this production. As a result, many rare and local domestic breeds are on the verge of extinction. A survey published by the FAO in 2007 (http://ftp.fao.org) lists 742 pig breeds, of which 137 are extinct and another 130 are endangered, all of which are local or rare breeds (Table 1).

Over the past two decades, several studies have attempted to characterize the genetic diversity of domestic pig populations to establish whether their loss poses a threat to future breeding programs owing to irretrievable loss of unique genetic variants. These studies make use of different genetic techniques, such as microsatellite (104, 105, 142–145), mtDNA (102, 103, 146), and AFLP markers (147, 148).

Unlike European pigs, Chinese breeds harbor a clear geographical structure (105). Clustering within Europe generally shows a clear difference between pigs from the United Kingdom and Mediterranean countries, most likely as a result of the importation of Chinese domestic stock into the United Kingdom during the Industrial Revolution. These results are confirmed by more
Table 1: Conservation status of local breeds in the world*

<table>
<thead>
<tr>
<th>Region</th>
<th>Critical</th>
<th>Critical-maintained</th>
<th>Endangered</th>
<th>Endangered-maintained</th>
<th>Extinct</th>
<th>Not at risk</th>
<th>Unknown</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Africa</td>
<td>NA</td>
<td>NA</td>
<td>4</td>
<td>NA</td>
<td>NA</td>
<td>22</td>
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<td>7</td>
<td>4</td>
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<td>6</td>
<td>15</td>
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<td>8</td>
<td>53</td>
<td>18</td>
<td>90</td>
<td>55</td>
<td>28</td>
<td>279</td>
</tr>
<tr>
<td>Latin America</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>NA</td>
<td>7</td>
<td>43</td>
<td>60</td>
</tr>
<tr>
<td>Near and Middle East</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td>1</td>
</tr>
<tr>
<td>North America</td>
<td>2</td>
<td>NA</td>
<td>1</td>
<td>NA</td>
<td>NA</td>
<td>1</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>Southwest Pacific</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>1</td>
<td>15</td>
<td>17</td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td>16</td>
<td>71</td>
<td>25</td>
<td>106</td>
<td>202</td>
<td>195</td>
<td>654</td>
</tr>
</tbody>
</table>

*These numbers are only for local breeds that are unique to each region (row). Critical-maintained and endangered-maintained mean those conservation efforts are ongoing. The raw data were obtained from the Food and Agriculture Organization of the United Nations [http://dad.fao.org/](http://dad.fao.org/).

Recent studies using a panel of 60K SNPs (38, 106). Although these studies provide a good general overview of diversity and relatedness, they do not provide an answer to the extent of the number of specific unique variants within these different breeds.

With the increasing number of pigs whose complete genome has been sequenced (38, 39, 41, 149), however, this kind of information is now becoming readily available, and it is now possible to investigate the genetic diversity of European pig domestic stock. Such large-scale genome-sequencing projects have revealed that the genetic diversity of European local and rare breeds varies considerably (i.e., Iberian pigs, Mangalitsa from Hungary, or Casertana from Italy).

These variations most likely are due to different degrees of introgression from Chinese pigs (149). Nevertheless, the genetic diversity of European domestic pigs is much greater than that found in European wild boar, most likely as a result of the introgression from Chinese pigs into European stock (38, 113, 150). Rare breeds in Europe have their own, unique genetic ancestry, as revealed by a large-scale assessment of nonsynonymous mutations (149). Moreover, genome sequencing of a few rare breeds, such as Mangalitsa, Casertana, Calabrese, and Iberian, revealed that these populations harbor over 10,000 unique genetic variants not found in current commercial breeds (M.A.M. Groenen, unpublished results). This suggests that conservation of rare breeds is critical because they are a key reservoir of genetic variation that may be important for future breeding programs.

Wild boar populations are also a reservoir of genetic variation. However, in Western Europe, many regions where the local populations have gone extinct (e.g., from overhunting) have been recently restocked with wild boar populations derived from elsewhere (151, 152). This process resulted in a dramatic loss of genetic diversity compared with that of domestic breeds and wild boars in Asia (38, 39, 153). Until the late Middle Ages, pig breeding in Europe was characterized by ongoing admixture with wild boar (115), suggesting that much of the wild boar variation is present in modern domestic breeds. However, a comparison of the genome sequence of 38 European wild boars and 169 European and Asian pigs revealed 142,249 SNPs found only in European wild boar (M.A.M. Groenen, unpublished results). This suggests that wild boar, and
especially Asian populations, likely harbor a significant amount of genetic variation not found in domestic populations. Conserving wild boar in Europe is therefore important not only for their survival but also to provide future generations with the necessary power to breed better, more resilient domestic pigs.

**CONCLUSION**

Since the Oligocene, Suidae lineages have undergone many rounds of adaptation, reticulation, expansion, and species replacement. Their history has been made more complicated by thousands of years of interactions with humans as prey, by being translocated, and as a domestic animal. Anthropogenic influences on suids, including deforestation, hunting, and translocation, have also resulted in loss of biodiversity due to population decline and, often, hybridization. In addition, recent changes in industrial pork production systems have resulted in a loss of genetic diversity in numerous regional domestic populations, threatening future breeding efforts.

The Suidae are also an excellent model to study speciation and domestication. Genomics of suids have shown that both of these processes involved a substantial amount of hybridization. What remains unknown, however, is the degree to which these reticulations were adaptive and provided suids with the phenotypic plasticity to rapidly adapt to novel natural and artificial environments.

Domestication and speciation are often considered distinct processes. The study of Suidae paleontology, archaeology, and genomics is allowing for an in-depth comparison of these two evolutionary phenomena and is leading to a greater appreciation for the role that hybridization and admixture play in both processes. The future of suid research therefore holds many promises for our understanding of the basic processes that generate the biodiversity on earth.

**DISCLOSURE STATEMENT**

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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