

The Evolution of CATS

Genomic paw prints in the DNA of the world's wild cats have clarified the cat family tree and uncovered several remarkable migrations in their past

By Stephen J. O'Brien and Warren E. Johnson

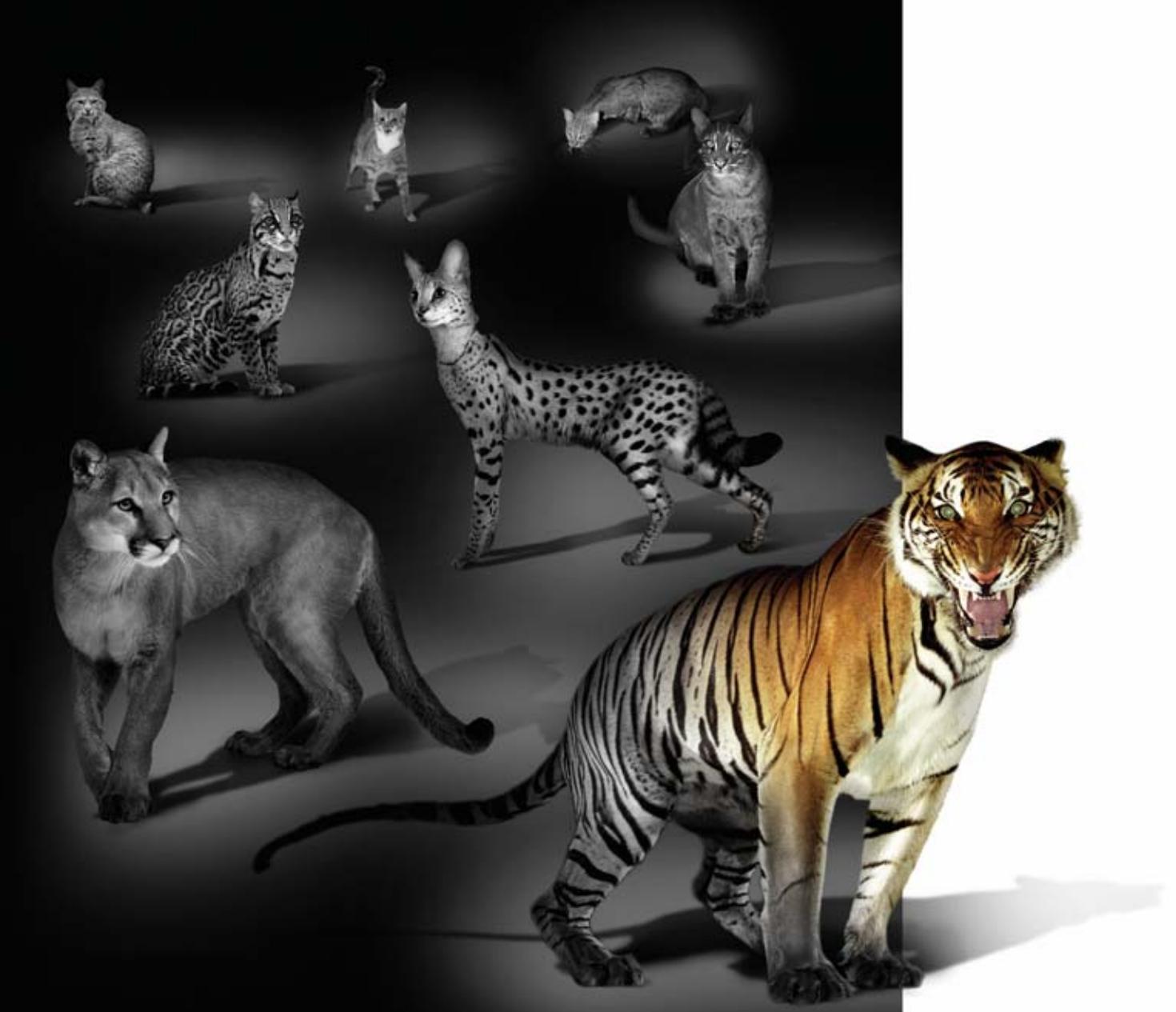
KEY CONCEPTS

- The family history of the cat has been murky because cat fossils are sparse and difficult to tell apart. But advances in the study of DNA have made it possible to construct the first clearly resolved family tree for cats.
- The DNA evidence shows that all living cats trace back to a pantherlike predator that lived in Southeast Asia 10.8 million years ago. The great roaring cats were the first to branch off; seven other lineages followed.
- As sea levels rose and fell, cats migrated to new continents and developed new species. A diminutive wildcat in the Near East was domesticated 8,000 to 10,000 years ago.
- Despite their evolutionary success, almost all wild cats are now threatened with extinction. —The Editors

Elegant and enigmatic, cats tantalize not only those of us who share our sofas with the smaller versions but scientists who have tried to puzzle out the origin and evolution of their larger cousins. Where did the modern cat family evolve? Why and when did they leave their homes and migrate across continents? How many species actually exist, and which ones are closely related?

Experts generally agree that there are 37 species in the family Felidae, but they have offered dozens of classification schemes, ordering cat species in as few as two to as many as 23 genera. Who could argue? Under the skin, one cat species appears pretty similar to another. They look like big cats, midsize cats and small cats. Distinguishing a lion's skull from a tiger's can be a challenge even for an expert, and genetic investigations that we have tried over the past two decades have failed to sort the cats into definitive groupings.

In recent years, however, a revolution in sequencing the genomes of various creatures, spearheaded by the Human Genome Project and by powerful technologies to probe DNA, has provided some extremely valuable new tools for inquiry. Drawing on



PHOTOILLUSTRATION BY JAMES PORTO; LEFT TO RIGHT: DULUC Corvix (bobcat); RUSSELL GLENISTER image00/Corvix (domestic cat); TERRY WHITE/TAKER Frank Lane Picture Agency/Corvix (gray-spotted cat); ZAINAL ZAHARI ZAINUDDIN (Asian golden cat); GETTY IMAGES (leopard); DANIEL ESTRIENE Getty Images (tiger); DANIEL J. FOX/Corvix (puma); DAVID KING/Getty Images (cheetah)

these novel techniques, the two of us, aided by colleagues at other institutions, have now constructed the first clearly resolved Felidae family tree. By comparing the same DNA sequences of 30 genes in each living cat species, we were able to determine the branches of the tree. Then, to arrive at the time each branch emerged, we used securely dated fossils and “molecular clock” analyses (which, based on the extent of differences in given genes, can estimate how long ago species diverged from one another). The result provided the first definitive look at how cats of all sizes are related to one another and led us to discern how and when these superb predators colonized five continents.

A Sense of Order

We immediately noticed that the DNA studies seemed to group the 37 species into eight distinct clusters, or “lineages.” We were fascinat-

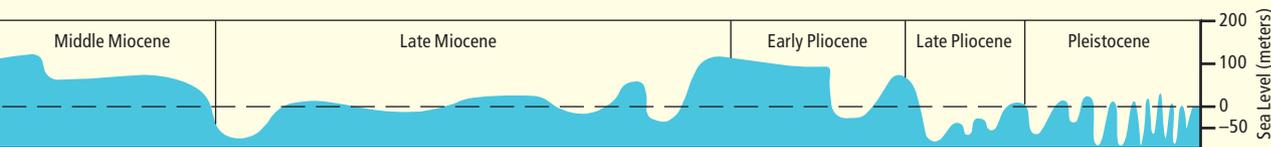
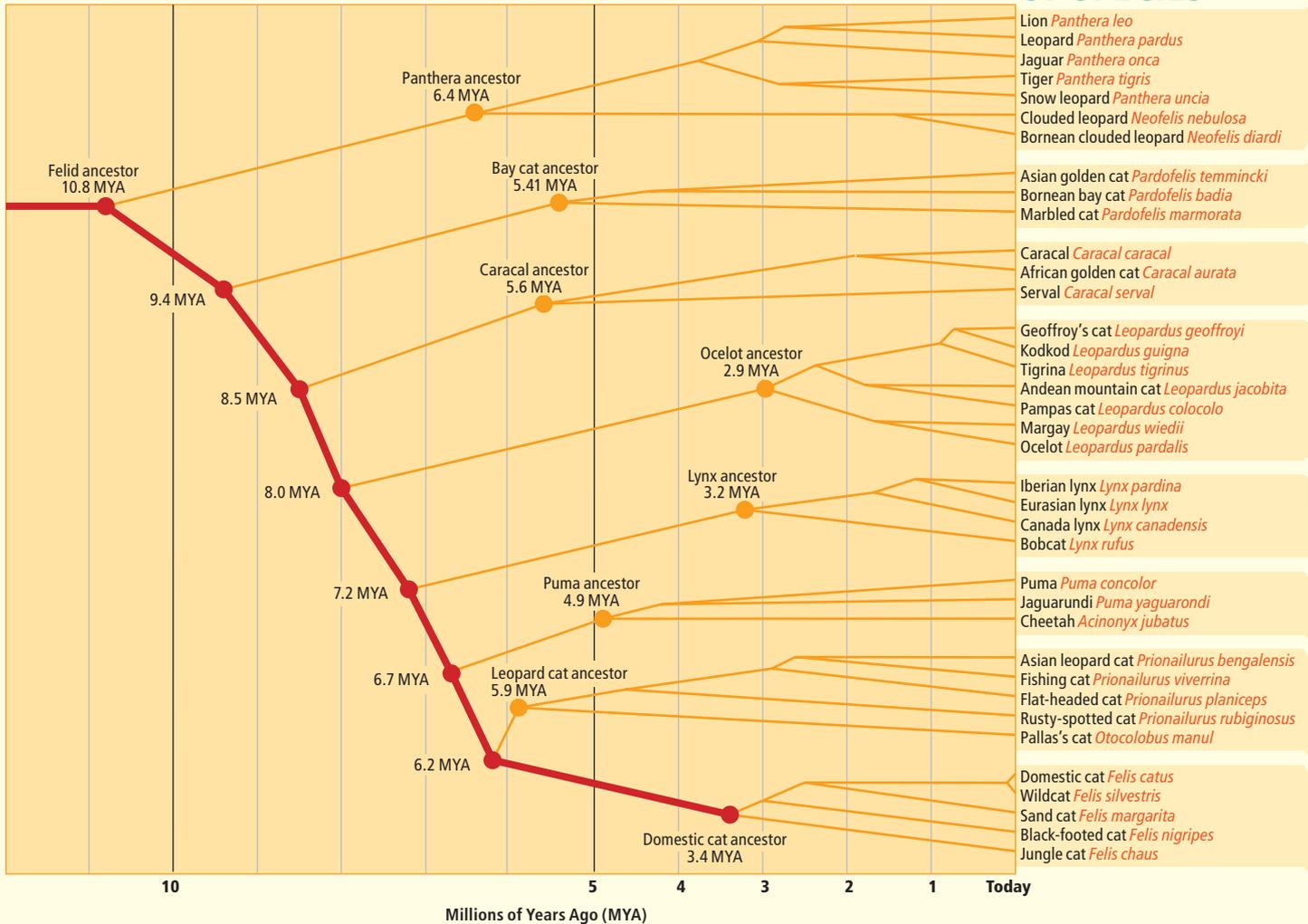
ed—and encouraged—to see that the eight groups defined exclusively by molecular analysis agreed with other kinds of observations, such as that species in one lineage often shared morphological, biological and physiological characteristics found only in their group. For example, one lineage contains all the great roaring cats (lion, tiger, leopard, jaguar and snow leopard). An incompletely ossified hyoid, a bone in the neck that supports the tongue, is what allows them to roar. Also in this group are the clouded leopard and the Bornean clouded leopard, little-known midsize cat species with a beautiful marbled coat; because they have a somewhat different bone structure in the neck, they cannot roar.

The comparison of gene sequences identified the lineages, the order of their emergence and, with the help of fossil calibrations, the time they appeared. Nevertheless, we needed two

THE CAT FAMILY TREE

Scientists compared DNA sequences in all 37 species of cats to determine the tree's branches. Fossils provided dates that indicate when major branching occurred.

37 SPECIES



additional pieces of information to fill out our scenario and discern where cats first arose and how they came to have their current distribution around the world. First, we determined the present distribution of each cat species and where their ancestors occur in paleontological remains. Then we looked at the cats' world through the eyes of geologists who have interpreted the composition of sedimentary deposits to infer the rise and fall of sea levels. When sea levels were low, land bridges connected continents, allowing mammals to migrate to

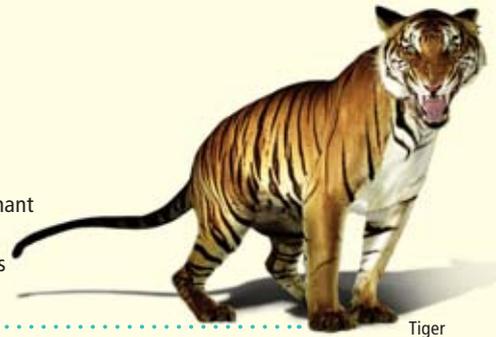
new domains. When sea levels rose again, animals on the continents were isolated once more. Studies of vertebrates show that isolation on continents, or on islands, provides just what is required for a population to drift apart so much genetically that eventually it can no longer breed with contemporary descendants of its former relatives—a reproductive distancing that is the hallmark of speciation. Armed with these pieces of the puzzle, we could construct a plausible sequence of migrations throughout the history of Felidae.

JANA BRENNING

8 LINEAGES

1 PANTHERA

These medium- to large-size cats (15 to 350 kilograms) are found throughout the world. They are the dominant predators in the ecosystems and on the continents that they inhabit, often specializing on large ungulate species. The lion, tiger, jaguar, leopard and snow leopard have an incompletely ossified hyoid, which allows them to roar. The two clouded leopard species do not roar.



Tiger

2 BAY CAT

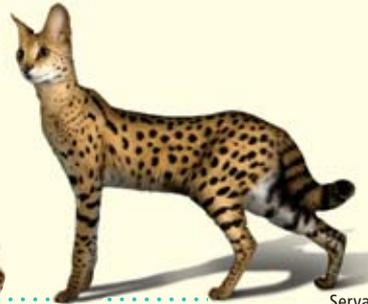
This poorly known group of small- to medium-size cats (two to 16 kilograms) is restricted to forested habitats in tropical Southeast Asia. Before the authors' genetic analyses, taxonomists did not consistently group these species together.



Asian golden cat

3 CARACAL

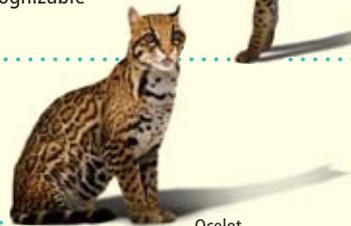
These medium-size cats (five to 25 kilograms), which are restricted to Africa, are distinctive and recognizable but were not typically grouped together before the authors' genetic work.



Serval

4 OCELOT

These small- to medium-size cats (1.5 to 16 kilograms) live in a broad range of habitats throughout Central and South America. They have a different number of chromosomes than other Felidae species do (36 instead of 38).



Ocelot

5 LYNX

These medium-size cats (six to 20 kilograms) all have short tails and pointed ears. They live in temperate climates of North America and Eurasia and tend to specialize on hare and rabbit. With the exception of the Iberian lynx, these species have been among the most widely exploited for their fur.



Bobcat

6 PUMA

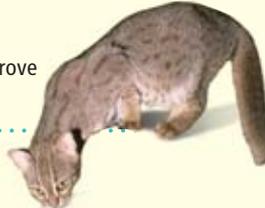
These diverse cats, from the small jaguarundi (three to 10 kilograms) to the large African cheetah (21 to 65 kilograms), originated in North America but have spread widely across four continents and remain broadly distributed. Pumas can be locally common and are legally hunted in parts of their range.



Puma
(mountain lion)

7 ASIAN LEOPARD CAT

These small cats (two to 12 kilograms) occupy a wide range of habitats in Asia, from mangrove forest to Mongolian steppe. The Asian leopard cat is the most common small cat in Asia.



Rusty-spotted cat

8 DOMESTIC CAT

These small cats (one to 10 kilograms), with the exception of the domestic cat, which is worldwide, have African and Eurasian distribution.



Domestic cat

Based on the fossil record alone, most researchers have accepted a cat called *Pseudaelurus* that lived in Europe nine million to 20 million years ago as the last common ancestor of modern felids. (*Pseudaelurus* was not the first cat; large saber-toothed cats, called nimravids, reach back as far as 35 million years ago, but nearly all their descendants went extinct.) Our recent molecular investigations, however, suggest that all modern cats are descended from one of several *Pseudaelurus* species that lived in Asia some 11 million years ago. Although we

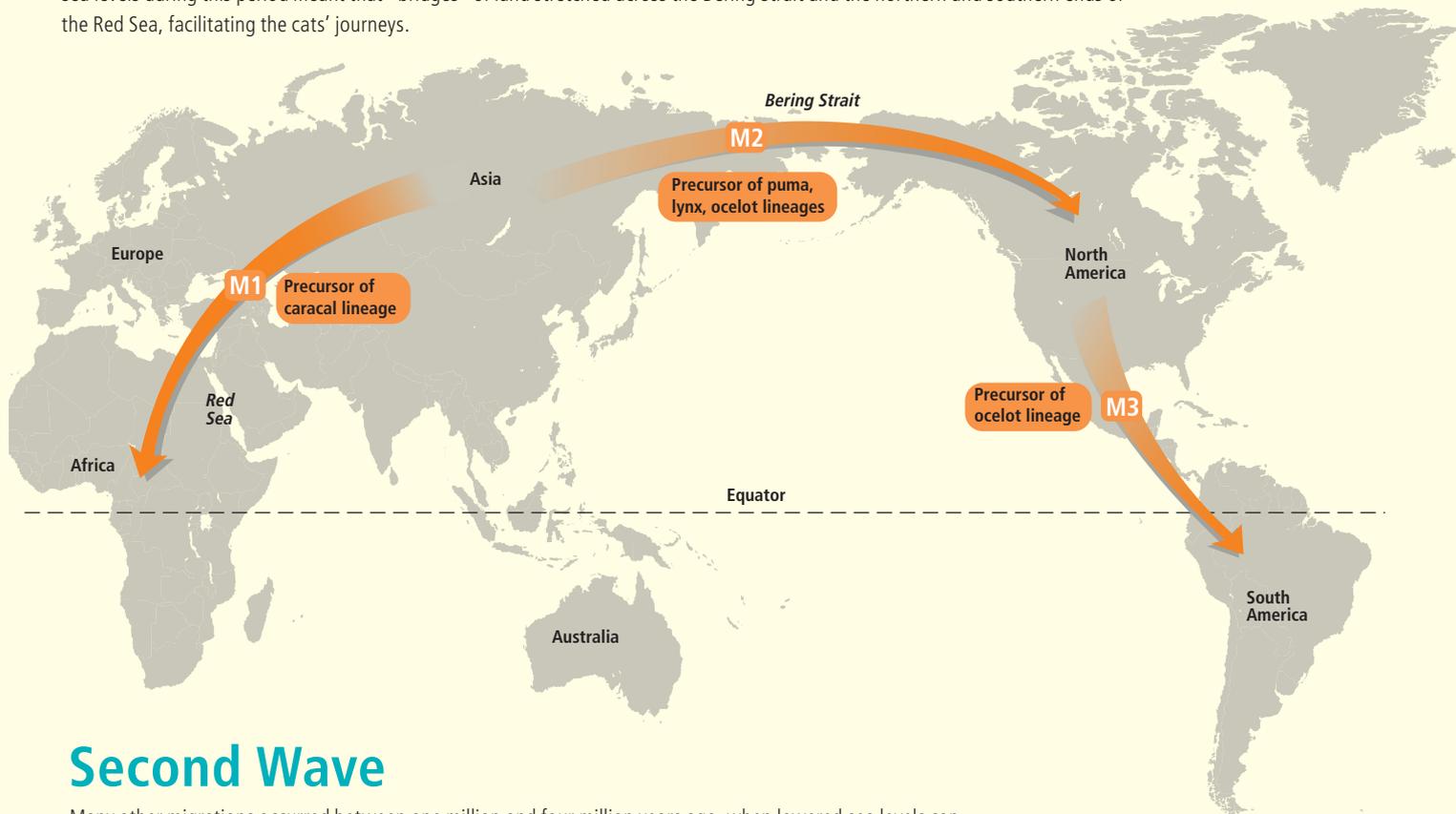
are not certain which exact species this ancestral cat was, we do believe that the ancient group included the Adam and Eve of today's 37 species of Felidae.

On the Move

The first group branched off from this mysterious Asian cat approximately 10.8 million years ago, producing the panthera lineage **1** [see table above], which today includes the great roaring cats and the two species of clouded leopard. A second split about 1.4 million years

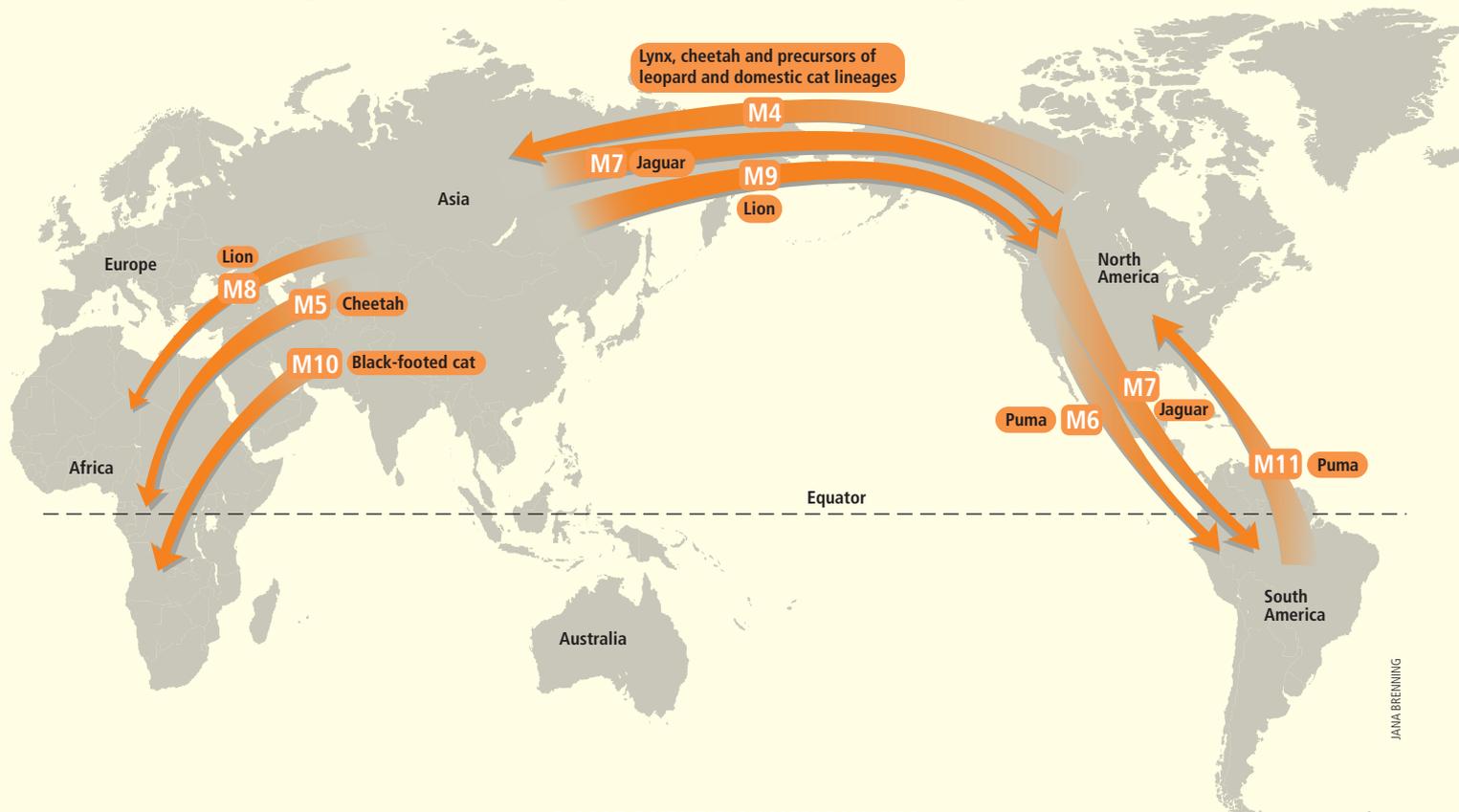
First Wave of Feline Migrations

Sometime around nine million years ago descendants of the pantherlike predator that is the ancestor of all modern cats began to migrate from its home in Asia to Africa (M1) and North America (M2) (and very much later to South America (M3)). Unusually low sea levels during this period meant that "bridges" of land stretched across the Bering Strait and the northern and southern ends of the Red Sea, facilitating the cats' journeys.



Second Wave

Many other migrations occurred between one million and four million years ago, when lowered sea levels connected the continents once again. The most recent puma migration (M11) occurred 8,000 to 10,000 years ago.



[THE AUTHORS]



After receiving a doctorate in genetics at Cornell University in 1971, **Stephen J. O'Brien** joined the National Cancer Institute as a postdoc. He is now chief of the NCI's Laboratory of Genomic Diversity, which he founded in the late 1980s. This is his fourth article for *Scientific American*. His most recent book is *Atlas of Mammalian Chromosomes* (Wiley, 2006). **Warren E. Johnson** earned his Ph.D. in animal ecology from Iowa State University in 1992 and joined the Laboratory of Genomic Diversity that same year.

later, also in Asia, led to the Bornean bay cat lineage 2, now composed of three small cats that evolved and still reside in Southeast Asia. The next split from the original group founded the caracal lineage 3, today represented by three midsize species whose progenitors crossed into Africa eight million to 10 million years ago, embarking on the first intercontinental migration [see upper map on opposite page]. During this period, sea levels dropped to 60 meters below modern levels, connecting Africa and the Arabian Peninsula by land bridges at either end of the Red Sea and facilitating the migration to Africa.

Cats migrate because their hardwired behavior demands dispersal every generation. Once they reach adolescence, young males, and occasionally females, are forced to vacate their natal area. So, over time, growing cat populations require greater and greater territory for expansion. This behavior, together with the pressure to follow migrating prey species, probably explains why cats have been motivated to travel far and wide. They are also extremely skillful predators and quickly explore new regions as opportunities arise, so it is not surprising that they can move into unexploited areas successfully.

During the same interval in which Asian cats began to move into Africa, they also dispersed

across Asia and traversed the Bering land bridge to Alaska. As cats now prowled Asia, Europe, Africa and North America, sea levels rose, separating continents, and with the isolation and changing habitats, a score of new species evolved. In North America, the ocelot 4 and lynx 5 lineages separated from the original migrants eight million and 7.2 million years ago, respectively, with the ocelot lineage ultimately dividing into two species there and the other group producing four species: three lynxes and the bobcat. The puma lineage 6 diverged 6.7 million years ago, giving rise to the puma (also called cougar or mountain lion), jaguarundi and American cheetah. Fossil remains of all these species in American deposits nail down their origin in the Western Hemisphere.

Two million to three million years ago a new ice age caused the oceans to recede once again, enough, along with shifting landmasses, to connect the two American continents via the Isthmus of Panama. A few cats of this time grasped the opportunity to migrate, headed south and encountered a continent with no placental carnivores (no bears, dogs, cats, skunks, and so on). South America had been isolated from northern landmasses for tens of millions of years and was teeming with marsupial species, including several successful carnivorous varieties. But when

SHARON ANGLIN (O'Brien); NORBERT ROSING (National Geographic Image Collection); TOM BRAKEFIELD (Cats); (snow leopard); JOE McDONALD (Canada lynx); BEVERLY DOUBERT (National Geographic Image Collection (African lion)); TKOFOTO.COM (fishing cat); SA TEAM Foto Natural/Minden Pictures (jaguar)

WHERE THE CATS ARE TODAY

Region	Cat Species
Europe	European wildcat ▲, Iberian lynx
North Asia	Asiatic wildcat, Chinese mountain wildcat, Eurasian lynx, Pallas's cat, Snow leopard ▲
North America	Bobcat, Canada lynx ▲, Jaguar, Puma
Sub-Saharan Africa	African golden cat, African lion ▼, African wildcat, Black-footed cat, Caracal, Cheetah, Leopard, Serval
Tropical Asia	Asiatic golden cat, Asian lion, Bornean bay cat, Bornean clouded leopard, Clouded leopard, Fishing cat ▼, Flat-headed cat, Jungle cat, Leopard, Leopard cat, Marbled cat, Rusty-spotted cat, Sand cat, Tiger
South America	Andean mountain cat, Geoffroy's cat, Jaguar ▼, Jaguarundi, Kodkod, Margay, Ocelot, Oncilla, Pampas cat, Puma

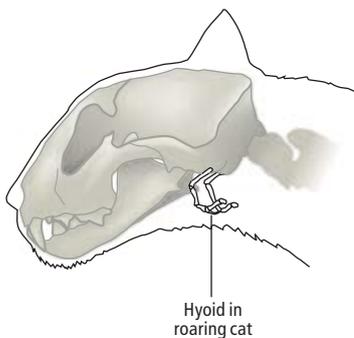
FAST FACTS

There are 600 million domestic cats around the world.

Cat fossils are so similar that even experts struggle to tell a lion's skull from a tiger's.



Lions, tigers, jaguars, leopards and snow leopards are the only cats that can roar. An incompletely ossified bone in the throat called the hyoid makes these unusual vocalizations possible.



the cats arrived across Panama, they had already become the ultimate predators: large, fast, dexterous, ferocious and deadly. The more modest marsupial carnivores were no match for them. Nearly all resident marsupials were quickly replaced by migrant carnivores such as cats of the ocelot lineage, which diversified still further in their new home, creating seven species that still survive in South America.

As the last ice age wound down about 12,000 years ago, the thick ice sheets that covered all of Canada and the northern tier of the U.S. gradually melted, transforming the barren landscapes into the forested terrain and grassland prairies of North America. After the big thaw, a cataclysm abruptly extirpated 40 species of mammals from North America. The Pleistocene extinctions, as they are called, eliminated 75 percent of the large animals living there. Mammoths, mastodons, dire wolves, massive short-faced bears, giant ground sloths, American lions, saber-toothed cats, pumas and cheetahs would all disappear from North America. Cheetahs escaped extinction because several million years earlier, when seas were still low, a number of their ancestors had made their way back to Asia [see lower map on page 72] and then Africa. Pumas avoided annihilation in a South American refuge and restocked North America many generations later. The other species would never return.

The Journey Continues

At roughly the same time the cheetahs made their way back across the Bering Strait from America to Asia, the precursors of the leopard cat 7 and the domestic cat 8 lineages slipped from their American roots and crossed the Bering land bridge to Asia. Subsequently, the leopard cat lineage blossomed to produce the Asian leopard cat and four small species that today are found in India (rusty-spotted cat), Mongolia (Pallas's cat), Indonesia (flat-headed cat) and other scattered Asian locales (fishing cat).

Also in Asia during this period, the great roaring cats of the panthera lineage spread much more widely than before. Massive 320-kilogram tigers ranged throughout southern and eastern Asia (India, Indochina, the Sunda Shelf and China), whereas in northern and western Central Asia, the snow leopards adapted to high elevations in the Himalayas and Altai Mountains. Leopards dispersed not only across Asia but also into Africa, where they occur today. Lions and jaguars traveled to North America dur-

ing the late Pliocene, roughly three million to four million years ago. Although the Pleistocene extinctions eliminated both species from North America, jaguars had escaped to South America, and lions, which had also dispersed to Africa, found a continent more hospitable than Europe, Asia or the Americas had been. The king of beasts clings to survival today in Africa, numbering fewer than 30,000 individuals. In Asia, lions are virtually extinct; only a tiny relict population of around 200 highly inbred Asiatic lions survives in the Gir Forest sanctuary in the Gujarat province of western India.

Our genetic analyses have also revealed a close call with extinction for tigers. Around 73,000 years ago the massive Toba volcanic eruptions on Borneo annihilated scores of mammal species in East Asia, including a widespread tiger population. A tiny group of tigers survived and repopulated a new race across the region, but the lack of genetic diversity in their modern descendants indicates the survivors passed through a population bottleneck at the time of the Toba eruption—leaving only a small group of animals to carry on the species. Like the cheetahs and pumas in North America, the tiger slipped through by a whisker.

Into Our Living Rooms

The final act in the cats' journey, from the jungle to our living rooms, began in the dense forests and vast deserts around the Mediterranean basin. There a handful of diminutive cat species (weighing less than 10 kilograms) had gradually emerged—the East Asian jungle cat, Middle Eastern sand cat, African black-footed cat and a ubiquitous wildcat species with four well-recognized subspecies (European, Central Asian, Near Eastern and Chinese). From one of these wildcat subspecies, one of the most successful experiments in history began—that of cat domestication. A wide-reaching molecular genetics study of the world's domestic cats and wildcats by graduate student Carlos Driscoll of the University of Oxford has brought this process into clear focus. All domestic cats carry genetic signatures matching Asian wildcats from Israel and the Near East.

We now believe that the cat was domesticated on several occasions, all within the Fertile Crescent 8,000 to 10,000 years ago, as nomadic human populations began to gather in small villages around the first agricultural settlements. These early farmers cultivated wheat and barley. Wildcats in the region, perhaps attracted by the

SOLVING THE CAT PUZZLE

Taxonomists have historically found it difficult to classify the cat family because the fossil record is sparse and it is hard to distinguish one fossil species from another. By analyzing the DNA of all 37 living species, the authors were able to sort the cat family into eight lineages. They obtained the DNA by collecting blood or tissue samples from each of the 37 species. Getting all the samples was not easy, because some of the species are rare and live in remote locations. They also analyzed seven “outgroup” species, close relatives of cats in the civet-mongoose family, Viverridae. The outgroup species provide a baseline for estimating the divergence dates within the Felidae family.

The scientists looked at DNA from the X and Y chromosomes and from the mitochondria (parts of the cell that generate energy and are passed along the maternal line). They focused on the DNA sequence of 30 different genes—in all, 22,789 nucleotide letters for each cat species. Nearly half of these sequences were variable across the range of species. The differences are what allowed investigators to determine which groups were most related and which were oldest. Genes accumulate changes over time. If these are not detrimental, they persist. So a species that emerged earliest would have had the most time for its genes to change and would show the most variation within any given gene, and one can safely assume that species whose genes share many of the same changes are most related.

Once the DNA analyses had allowed investigators



CINNAMON:
Her DNA was sequenced.

to resolve the branching nodes, or “forks,” in the cat family tree, they turned to fossils to estimate when the forks actually happened. Paleontologists have determined the age of dozens of fossils of ancient cats using radiocarbon-dating methods. Certain cat fossils considered as missing links (the most recent common ancestor of a group such as the great cats, lynxes or ocelots) provided 16 firm fossil dates for specific branch points on the tree. Then, mathematical computer scripts based on a steady cumulative molecular clock translat-

ed the genomic data into estimates of the time elapsed since each divergence node. (The molecular clock idea assumes that some evolutionary changes occur at a regular rate. Mutations, for example, may be incorporated in the DNA of genes at a steady rate over millions of years. Differences in the DNA, therefore, can act as a “clock” for measuring the date at which two lineages split from a common ancestor.)

The most recent addition to genome sequences is the complete set of genetic information in the DNA of an Abyssinian cat named Cinnamon. Cinnamon’s full genome sequence, along with the sequence of 32 other species of mammals (including human, mouse, dog, cow, elephant and representatives of most mammalian orders), has given students of evolution an almost unlimited assemblage of genetic information across the 100-million-year-old history of modern mammals.

—The Editors

plentiful rodents in the grain stores, apparently offered themselves as cautious companions, earning their keep by dispatching the pesky rodents. The increasingly tame wildcats bred prolifically and linked their fortunes to those of the humans.

These animals ultimately undertook a new migration. It began on foot, then progressed in wagons, and eventually on oceanic vessels, ultimately spreading the domesticated cat companions across the globe. Some 600 million domestic cats live worldwide today, almost the only cat species not considered threatened or endangered by the world’s conservation organiza-

tions. By the 19th century, cat owners were selectively mating their pet tabbies to produce fancy breeds. The American Cat Fanciers Association lists 41 official cat breeds, from Maine Coon to Siamese to Persian to Korat, all tracing their roots to the birth of human and feline civilization in the Fertile Crescent.

The evolutionary story that emerges from our studies of the cat family serves as a harbinger for the fledgling field of “genomic prehistory.” Just as for the cats, the patterns of genomic variation carried by each species contain footprints of kinship, migrations, bottlenecks and expansions across the planet. ■

➔ MORE TO EXPLORE

Wild Cats of the World. M. Sunquist and F. Sunquist. University of Chicago Press, 2002.

Tears of the Cheetah and Other Tales from the Genetic Frontier. S. J. O’Brien. St. Martin’s Press, 2003.

Phylogeography and Conservation Genetics of Tigers (*Panthera tigris*). S.-J. Luo et al. in *PLoS Biology*, Vol. 2, pages 2277–2293; 2004.

Big Cat Genomics. S. J. O’Brien and W. E. Johnson in *Annual Review of Genomics and Human Genetics*, Vol. 6, pages 407–429; 2005.

The Late Miocene Radiation of Modern Felidae: A Genetic Assessment. W. E. Johnson, E. Eizirik, J. Pecon-Slatery, W. J. Murphy, A. Antunes, E. Teeling and S. J. O’Brien in *Science*, Vol. 311, pages 73–77; 2006.