Skunks have an unfavorable reputation because the overpowering spray from their anal glands strikes our primal sense of smell. In his journal on the Beagle voyage, while passing the night in Punta Alta, Argentina, Charles Darwin noted:

We saw also a couple of Zorillos, or skunks,—odious animals, which are far from uncommon. In general appearance the Zorillo resembles a polecat, but it is rather larger, and much thicker in proportion. Conscious of its power, it roams by day about the open plain, and fears neither dog nor man. If a dog is urged to the attack, its courage is instantly checked by a few drops of the frigid oil, which brings on violent sickness and running at the nose. Whatever is once polluted by it, is for ever useless. [Félix de] Azara says the smell can be perceived at a league distant; more than once, when entering the harbour of Monte Video, the wind being off shore, we have perceived the odour on board the Beagle. Certain it is, that every animal most willingly makes room for the Zorillo. [The Voyage of the Beagle]

If a hungry predator, often many times larger than a skunk, can be deterred by a misty spray, one has to marvel at nature’s creativity.

Skunks, in the order Carnivora, were classified until fairly recently as part of the family Mustelidae, which includes weasels (genus Mustela, the name bearer of the family), badgers, martins, otters, and wolverines, among others. Many mustelids have an anal scent gland that produces a pungent secretion used as a defensive weapon, a seemingly obvious connection to the skunks. The apparent relationship was further reinforced by additional shared physical characters, such as the evolutionary loss of the last upper and lower molars (the wisdom teeth in humans) and the
lack of a carnassial notch (a slit in the upper fourth premolar). Indeed, as Darwin remarked, the skunk looks like a polecat, a typical example of a mustelid.

That conventional wisdom, however, came under challenge during the past fifteen years, when DNA data became widely available. With mounting genetic evidence, initially based on mitochondrial DNA (mtDNA) and increasingly on nuclear DNA, it has become apparent that skunks do not belong to the Mustelidae but form a family of their own, the Mephitidae. Indeed, they fall outside a clade, or evolutionary descent group, that includes not only the weasel family but also the raccoon family (Procyonidae) and the red panda family (Ailuridae).

Modern skunks have a modest diversity in the New World, composed of 12 named species of spotted skunks (genus *Mephitis*, two species), spotted skunks (genus *Spilogale*, four species), and hog-nosed skunks (genus *Coepitrapus*, four species). Less familiar (at least to Westerners) are the Southeast Asian stink badgers (genus *Mydaus*, two species), which, as implied in their common name, have long been thought of as badgers but are actually skunks.

One of the key morphologic characters of the skunk family is an enormous enlarged chamber in the middle ear region. In mammals the middle ear is enclosed by a rounded bony enclosure called the tympanic bulla, with the eardrum at its entrance. Air-borne sounds received by the eardrum are transmitted through three tiny bones (called auditory ossicles) into the inner ear, where the vibrations are sensed by nerves and converted into electrical impulses that are sent to the brain. The middle ear space is filled with air. In part that is to balance the pressure outside the eardrum, but the volume of the air space also affects sensitivity to certain frequencies of sound, presumably enhancing those that are most important to the mammal in question.

Some mammals have evolved an enlarged air space, which improves the perception of low-frequency sounds. The most straightforward way to create the extra space has been to simply enlarge the size of the bulla, ballooning it ventrally, as is seen in the desert fenec fox (*Vulpes zerda*). Skunks, however, have expanded the air space sideways—instead of the bulla, the lateral characters of the braincase have become inflated through evolution. That characteristic is evident on the external morphology of the skull and is often preserved in the fossil record. So far as we know, it is uniquely possessed by stink badgers and skunks.

Another clue that skunks form their own family is that their lower first molar (the lower carnassial) has a distinct third root originating just below the outer gum line (other members of the Carnivora have two roots on all their carnassials). Such a root is often very small and easily overlooked, but is consistently present in all known living and fossil skunks (see photograph on opposite page). With the above two “hard” features (preserved in bones), paleontologists can unambiguously identify a fossil skunk, even though its anal gland is never preserved in the fossil record.

Using estimates of DNA sequence divergence, popularly called the molecular clock, biologists estimate that the skunk family originated sometime between 34 million and 32 million years ago. Fossil evidence for the skunks, however, is nowhere nearly as old. In 1999, Mieczysław Wolsan, a vertebrate paleontologist at the Polish Academy of Sciences, reevaluated a rather strange-looking carnivore cranium from Europe, first described 160 years before. The fossil dates from the middle Miocene epoch (about 12 million years ago). When first described it had been thought to be a skunk, as reflected in its name, *Palaeomephitis*. However, others had since questioned that identification, concluding it was a type of civet. Wolsan reaffirmed the original identification, and concluded the cranium is the oldest skunk fossil on record. If the molecular clock is correct, that means either that there is a large gap in the fossil record or that paleontologists have failed to recognize skunk fossils currently sitting in museum collections.

A far better known genus than *Palaeomephitis* is *Promephitis*, an animal the size of a modern striped skunk. Its fossils occur in much of Eurasia and are especially abundant in the Linxia Basin in Gansu Province, north China. They date from 11 million to 3 million years ago, that is, during the late Miocene and well into the Pliocene epoch. Despite that long record, however, *Promephitis* is probably not a direct ancestor of the living Southeast Asian stink badgers.

The stink badgers offer a different example of the difficulty in correctly identifying external characters for classification. Unlike skunks, the lateral characters of the braincase have become inflated through evolution. That characteristic is evident on the external morphology of the skull and is often preserved in the fossil record. So far as we know, it is uniquely possessed by stink badgers and skunks.

Another clue that stink badgers form their own family is their second lower molar (the lower carnassial). Unlike skunks (which vaguely resemble those of the badger family *Meles*), stink badgers have two roots on their lower first molar (arrow). In other members of the order Carnivora, that tooth has two roots.

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**Evolutionary tree of the Caniformia (lower diagram) shows the relationship of the families that make up one of the two main groups in the order Carnivora (the other group is the Feliformia). Once thought to be members of the weasel family, skunks are more closely related to weasels than they are to red pandas and raccoons. Top diagram: Skunk lineages are plotted in time from their origin in the Old World to the present (thick bars indicate direct fossil or living evidence).**
the skunk family. Notably, however, it has the requis
site enlarged middle ear re

gion and an extra root on its lower first molar. All in all, it is close to what the ances
tor of all living New World skunks must have looked like, though we can't say it was the direct ancestor.

Based on molecular and fossil evidence, it is likely that the skunk lineage origi
nated in Eurasia and that one of its members—Martinogale or something very much like it—crossed into North America at a time when sea levels were low, exposing the so-called Bering Land Bridge. Since both living New World skunks and the Old World stink badgers possess anal scent glands, it is reasonable to assume that Martinogale did too. Based on the coat patterns of liv
ing New World skunks, we can also reasonably infer that Martinogale had dark hair with patches of white in stripes or spots (or at the very least one patch of white, as in the stink badgers). In living skunks, a large, bushy tail is confined to the New World, so most likely Marti
ogale's tail was more modest [see artist's reconstruction on pages 22–23].

Martinogale was one of the smallest of skunks, about six inches long (excluding the tail), weighing only about seven ounces. (Only the living pygmy spotted skunk, Spilogale pygmaea, is smaller or about the same size.) It probably fed on a mixed diet of small rodents (such as mice), insects, and worms. After arriving in the New World, Martinogale (or its equivalent) did not immediately begin to diversify. It kept a low profile for the next several million years, giving rise to one or two species only. Eventually we see a transitional form called Buisnictis, found in fossil deposits in Kansas,

Nebraska, Oklahoma, and Mexico from about 5 million to between 2 million and 1 million years ago, from the early Pliocene into the Pleistocene epoch.

Using mtDNA, Jerry W. Dragoo, a mammalogist at the University of New Mexico, Albuquerque, suggests that spotted and striped skunks are closely related to each other, to the exclusion of the hog-nosed skunks. Dragoo, by the way, is a great champion of skunks, via his Dragoo Institute for the Betterment of Skunks and Skunk Repu
tations (dragoo.org). My own research, based on the morphology of fossil and

preserved skull from the Red Rock Canyon State Park in the Mojave Desert of California (it was discovered by a field party under the supervision of a member of my team from the Natural History Museum of Los Angeles County). We described this late Miocene fossil in 2005. It is between 9.2 million and 9.3 million years in age and possesses some of the most primitive morphology for Martinogale's skull and other anatomical features suggest that it is closely related to modern skunks.

The next stage of New World skunk evolution is the diversification of the modern skunk genera and close relatives. An ancestor of hog-nosed skunks and a spotted skunk-like form appeared in the early Pliocene records of Mexico. Shortly af

ter that, the hog-nosed skunks managed to migrate into South America, tak

ing advantage of a newly formed land bridge connecting North and South America. This is part of a major geo
logic event called the Great American Biotic Interchange, or GABI, and hog

nosed skunks were among the earliest carnivores to expand to the south.

Molina's hog-nosed skunk, Conepatus chinga, a South American species, is adapted for digging and rooting for insect prey. It is one of four species of hog-nosed skunks, which together range from Texas to Southern Argentina.
modern skunks, indicates instead that striped and hog-nosed skunks are more closely related. Morphologically, these two skunk genera share many advanced features in their teeth and skulls, while spotted skunks appear to be relatively conservative in their dental morphology. Is this another case of appearances deceiving us on skunk relationships? If the molecular evidence is correct, then features shared by striped and hog-nosed skunks must have been independently acquired, an example of evolutionary convergence.

The modern species of skunks in North America—the spotted and striped species and one hog-nosed species—mostly appeared during the Pleistocene, as it is often the case for other mammals that live in North America. That epoch, also known as the Ice Age, lasted from about 2.6 million to 10,000 years ago. During that time a northern continental ice sheet repeatedly advanced and retreated, reaching southward as far as parts of Kansas, Illinois, Pennsylvania, and New York. The oscillating environments were so extreme that mammals had to constantly contract their ranges (during glacial maximums) and expand them (during interglacials) just to stay within their optimal habitats.

In such a fast-changing environment, Central America and southern North America may have acted as refugia for spotted skunk evolution. Of the two species of modern spotted skunks in the United States, the eastern spotted skunk (Spilogale putorius) and the western spotted skunk (S. graciosil), as their common names indicate, occupy roughly the eastern and western halves of the country. The late Richard van Gelder, a mammalogist at the American Museum of Natural History, suggested that their respective ancestral populations in their southern refugia expanded northward on the heels of the last glacial’s retreat. Their northward expansion has apparently continued during the last 100 years or so, because both spotted skunks have been documented to occupy progressively more northerly states during historic times, presumably because of a warming trend. (The enigmatic pygmy spotted skunk, S. pygmaea, is confined to the southern Pacific coast of Mexico.)

After all of that shuffling, however, “A Skunk’s A Skunk For A’ That.” Above all, skunks are still characterized by their possession of an anal gland capable of ejecting highly volatile, objectionable liquid. One of the extraordinary features of their evolution is that despite following separate lineages for as long as 30 million to 40 million years, the skunk family and the weasel family independently evolved to use their anal scent glands for defense. We can’t rule out the possibility that the common ancestor of skunks, weasels, raccoons, and red pandas had that ability, and that it was subsequently lost in the raccoons and red pandas. Evolutionarily speaking, however, that would be less likely, since it assumes three events instead of two (the acquisition of the trait by the ancestor and the subsequent loss by both raccoons and red pandas).

The moral of our skunk tale seems to be that in trying to gain insight, biologists have sometimes overrated their sense of smell (wrongly placing skunks in the Mustelidae) or undervalued it (failing to recognize stink badgers as skunks). In evolution, we risk errors if we only follow our noses.