SOPHIE CASSON/THREE IN A BOX

EVOLUTIONARY BIOLOGY

The lost appetites

Many vertebrates can detect the same five basic tastes that humans can, but there are exceptions. Are the differences caused by a change in diet?

BY EWEN CALLAWAY

Ronald Fisher must have been relieved when a chimpanzee at Edinburgh Zoo took a sip of water, looked him in the eye and spat at him.

It was August 1939, and Fisher was testing whether chimps could taste water laced with a chemical called phenylthiocarbamide (PTC) that some humans find nauseatingly bitter and others can't taste. Fisher and his colleagues Edmund Ford and Julian Huxley had been worried that the apes wouldn't make their preferences known, rendering the experiment pointless.

Instead, about three-quarters of the chimps they tested expressed their displeasure with PTC. Fisher's team speculated that the variation in sensitivity to bitter tastes was caused by a genetic mutation shared by humans and chimps, and that natural selection had maintained this diversity in both species. "Wherein the selective advantages lie, it would at present be useless to conjecture," the trio wrote[1] in a letter to *Nature*.

More than 70 years later, biologists are still trying to figure it out. The availability of different animal genomes has given scientists more insight, culminating in the startling discovery that, for many creatures, some tastes have no evolutionary benefit at all. Kurt Schwenk, a biologist at the University of Connecticut in Storrs who studies chemical sensing in lizards and snakes, says: "The whole story of the evolution of taste is really the evolution of loss of taste."

The most obvious explanation for the changes is lifestyle. At some point in evolutionary history, a shift in diet removed the need to sense certain chemicals in food. Evolution is a game of 'use it or lose it', and genes that do not aid an animal's survival or reproduction are liable to build up random mutations that destroy their ability to make a working protein. Gary Beauchamp, a geneticist at the Monell Chemical Senses Center in Philadelphia, Pennsylvania, likens the situation to that of sight in cave-dwelling fish. A life of darkness eliminated the usefulness of vision, so the fish collected mutations in genes involved in eye development and eventually lost their sight altogether.

Another example of taste loss lies closer to home: cats cannot taste sweet substances. Beauchamp noticed this quirk in the 1970s, and in 2005 his team finally found out why[2]. All cats share a mutation that disables one of the two genes that build a working sweet receptor, whether for the tongue, intestine or any other part of the body. Because all felines — from domestic cats to lions — have an identical mutation, it is likely that the sweet-receptor gene became inactive in their common evolutionary ancestor. Beauchamp speculates that this ancestral animal moved to a diet composed of protein-rich meat, devoid of sugary plants, negating the need for a sweet receptor.

Beauchamp's team recently discovered that the inability to taste sweetness is more widespread. They analysed 12 non-feline species belonging to the order Carnivora, including sea-lions, otters and hyenas, and identified crippling mutations in the sweet-receptor gene in 7 of them[3]. What's more, six species carried unique mutations, suggesting that the ability to taste sweetness had been lost repeatedly over the course of evolution. Presumably the mutations appeared after each species or its ancestors switched to a meat-only diet, Beauchamp says. This interpretation is supported by the team's finding that an omnivorous member of Carnivora, the spectacled bear, still has a working sweet receptor.

There may be other reasons why tastes are so dispensable. As well as lacking sweet receptors, dolphins also lack the ability to build working umami (which sense amino acids in proteins) and bitter taste receptors. One theory posits that because dolphins swallow their food whole, moderating their intake is irrelevant. However, this theory applies only to the ability to taste food, and ignores the role of these receptors in other parts of the body (see 'Hardwired for taste', page S7). There is no evidence that losing taste genes confers any advantages to an animal, although Schwenk is happy to speculate. "Most carnivores are scavengers as well as predators," he says. "They eat a lot of rotting flesh, so it might be good to not taste it so well."

Pandas, a largely vegetarian member of Carnivora, lack umami receptors. The pandas' bamboo-only diet gives them little need to detect proteins, says Jianzhi Zhang, an evolutionary geneticist at the University of Michigan in Ann Arbor, who reported this lack of receptors in 2010. His team also discovered that vampire bats have no sweet receptor, and that all bats, including insectivorous species, lack umami receptors[4]. Zhang's team has also been unable to find working sweet-receptor genes in several species of birds, grass-eating horses and omnivorous pigs — a pattern he finds puzzling.

DEVONIAN TASTES

The sense of taste must have carried an evolutionary advantage to have evolved in the first place. Beauchamp says that taste-sensing systems in the mouth perform two essential tasks: umami and sweet detection help animals find energy-dense nutrients, and bitter detection helps them avoid toxic substances. Scientists know far less about the biology and evolution of sour and salt tastes. One theory is that detecting salts helps an animal control its levels of sodium and other ions, whereas sour tastes help it avoid the acids in unripe fruit and spoiled foods.

All vertebrates have some ability to avoid toxic chemicals and seek out nutrients. By comparing animals from different branches of the evolutionary tree, scientists have inferred that taste probably evolved more than 500 million years ago — before land vertebrates, bony fish, sharks and lampreys diverged — when their common ancestor, a primitive fish, developed a new kind of cell.

Taste buds have been repeatedly tweaked over time to suit various animals' dietary needs, says Thomas Finger, co-director of the University of Colorado's Rocky Mountain Taste and Smell Center in Aurora. Many fish are covered with taste buds. "The super-tasters among the animal world are goldfish," says Finger. "Goldfish and catfish have way more taste buds than anybody else." They have poor vision, and their taste buds, including those on their whiskers, could help them sense their way to a meal in murky water, he adds.

The evidence suggests that umami receptors were the first to develop. In 2008, Zhang's team reported the discovery of genes, similar to those that encode receptors used by humans and mice to sense the amino acid glutamate, in the genome of the elephant shark, a species that branched off from other fish 400 million years ago. Sharks lack bitter taste receptors, suggesting that these genes evolved more recently.

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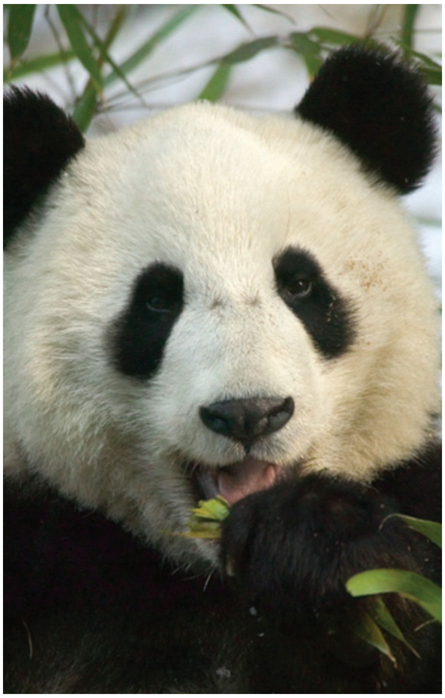
Bitter is perhaps the taste that most intrigues evolutionary biologists. It is the 'Darwin's finch' of taste, elaborated and customized to suit a species' ecological niche. Humans have 24 or 25 (depending on the person) different bitter receptors, each recognizing unique combinations of chemicals.



KEREN SU/ GETTY IMAGES

A strict bamboo diet might have stripped the panda of the umami taste receptor.

Toxic bitter compounds come in all shapes and sizes, so it makes sense that the receptors that recognize them are diverse, says Beauchamp. Bitterness is code for danger, but many bitter compounds also provide important nutrients. For example, during the lean winter months, the Japanese macaque supplements its diet by eating willow trees. The bark of the willow contains salicin, which tastes bitter to many animals. A recent study of the bitter receptor T2R16, which is common to all primates, reported that the macaque version is the least responsive to salicin[5].

Bitter taste evolution, then, is also about distinguishing between different chemicals. "If you go out into the real vegetable world, what you'll find is that almost everything is bitter," says Beauchamp. "An animal that rejects everything that's bitter would be in trouble."

This principle could explain Fisher's discovery that some individuals, among both humans and chimps, are unable to taste PTC. Seven decades later, researchers finally identified the gene responsible for PTC sensitivity, called *T2R38*, and confirmed that different versions of the gene largely explain why not everyone can taste the chemical (see 'The finer points of taste', page S2).

Recent studies have refined Fisher's ideas about how the variations in PTC sensitivity evolved. A team led by Stephen Wooding, an evolutionary biologist at the University of Texas Southwestern Medical Center in Dallas, repeated Fisher's experiments[6] using apples spiked with PTC, instead of water solutions (perhaps to avoid being spat at). Chimps still differed in their ability to taste the bitter chemical, but DNA sequencing revealed that chimpanzees that cannot taste PTC have an entirely different mutation in *T2R38* from human non-tasters — their insensitivity evolved independently.

One of the compounds that T2R38 recognizes, goitrin, is abundant in cruciferous vegetables, such as broccoli and Brussels sprouts. Goitrin can worsen hypothyroidism, a condition caused by low iodine intake. Variation in sensitivity to PTC and goitrin might persist because it could help iodine-starved populations avoid hypothyroidism and obtain nutrients from vegetables.

Diet is not the only driver of change in bitter-tasting ability, however. Geneticist Sarah Tishkoff's team at the University of Pennsylvania in Philadelphia recently tested[7] hundreds of individuals from 57 human populations in Central and West Africa. They found both PTC tasters and non-tasters, but there was no obvious correlation with their different diets.

In the past decade, scientists have discovered sweet receptors in the gut that influence insulin levels, and bitter receptors in the lungs that can clear inhaled substances. Tishkoff's team suggests that roles such as these, and not diet, might explain the evolutionary differences in PTC tasting. Zhang also thinks there is more to the evolution of taste than just flavour. He suggests that researchers use model organisms, such as mice lacking various taste genes, to understand the roles of these receptors. "We're finding a lot of mismatches between feeding ecology and taste-receptor evolution," he says. "Perhaps we still do not have a complete understanding of the functions of those genes — or of taste." ■

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