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Biomechanics: Squeezing power drives ballistic tongues

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Chameleons and lungless salamanders independently evolved very fast projectile tongues. In both cases, ballistic performance involves a long, blunt-ended skeletal rod that slides freely within a powerful squeezing muscle, without the need for exceptional material properties.

Tetrapods have evolved a diverse array of tongue adaptations to different modes of feeding¹. In many amphibians and reptiles, the tongue initiates prey capture by protruding from the mouth to grab or adhere to prey². Among species that project their tongues, an extreme form of performance evolved twice independently: the ballistic tongues of chameleons³ and some lungless salamanders⁴ (Figure 1). These tongues rapidly shoot out of the mouth, adhere to prey and are then retracted more slowly. This mechanism has many advantages: ballistic tongues minimise the chance of prey escape, conserve energy by allowing the predator to remain stationary, can hit targets that are otherwise hard to reach and maintain high performance at low temperatures⁵. In a new study in this issue of *Current Biology*, Yu Zeng and colleagues⁶ investigated which properties of the tongue-projection system were

modified during evolution to achieve extreme projection performance, and how this differs between the two groups.

One might expect that the extreme performance calls for extraordinary materials. Does the structure that powers the projection of the tongue — the accelerator muscle and its associated elastic tissues — outperform known biological materials? To identify what makes these tongue launchers special, Zeng and colleagues⁶ collected data from over forty species of chameleons and salamanders spanning a broad range of body sizes. They combined high-speed video analyses, anatomical investigations and biomechanical modelling. Surprisingly, the accelerator muscle's energy output fell at the lower end of muscle performance seen in jumping vertebrates. Its compressive stress during squeezing was also well within the typical range for

vertebrate muscle. So, if not due to the material properties of the muscle and its elastic tissues, how do chameleons and lungless salamanders reach such exceptional accelerations up to 5000 m/s² and speeds up to 5 m/s when launching their tongues?

The answer lies in the architecture of their launching system. Three functional modules came together in the ballistic tongues of chameleons and lungless salamanders: a long skeletal rod, a squeezer muscle with embedded elastic tissues that surrounds the rod and can extend over its tip as well as a loss of a fixed attachment between the muscle and the rod. This configuration persistently allows acceleration of the tongue through force exerted via squeezing on the rod's taper and tip. Zeng and colleagues⁶ show that shallow tapering and a blunt tip — features seen in ballistic-tongued species — improve

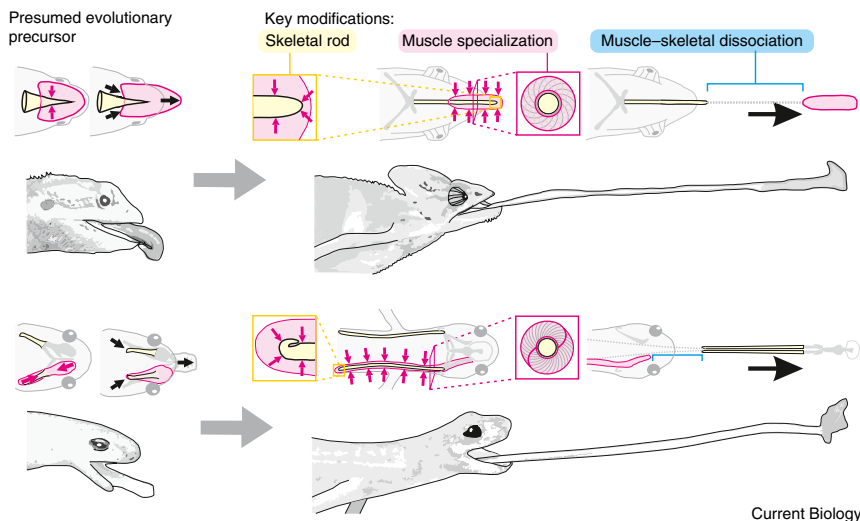


Figure 1. Convergent evolution of ballistic tongue projection in chameleons and lungless salamanders.

(Top left) In a likely ancestral state for chameleons, lizards such as agamids protrude their tongues by squeezing a tubular muscle (pink). The conically tapered skeletal element (yellow), around which the tongue muscle wraps, makes the tongue slide forward at relatively low speed as it contracts. (Top right) Three key modifications enable high-speed tongue projection in chameleons: the skeletal rod becomes elongated, shallowly tapered, and blunt ended. The muscle evolves into a powerful accelerator containing collagenous sheets and sheaths (magenta in cross-section) that store and release elastic squeezing energy³. The tongue and accelerator muscle become detached from the skeletal rod, which they push against during projection. (Bottom left) In a presumed ancestral state for lungless salamanders, newts protrude the tongue by pulling the tongue skeleton forward. (Bottom right) Convergence to the same key mechanical modules as for chameleons enables ballistic tongue projection in lungless salamanders. In contrast to chameleons, the skeletal rod is propelled forward along with the tongue, while the accelerator muscle remains anchored in place (bottom salamander drawn after a picture from²).

propulsion efficiency compared to skeletal shapes of non-ballistic tongued species.

Chameleons and lungless salamanders independently evolved these three key traits. However, the sequence of trait assembly was presumably different in the two groups. The chameleon lineage most likely evolved the muscle–skeletal dissociation early to aid in small-range tongue protrusion, as seen in *Pogona* (Figure 1). Modifications to the skeletal element and the development of elastic tissues in the muscle followed later. In salamanders, by contrast, the tongue skeleton probably already possessed a thick, blunt-ended form suitable for launching in taxa that pulled the tongue forward, such as in *Taricha* (Figure 1). Dissociation from the rod and the addition of elastic elements evolved later. Despite converging on these key mechanical traits, the morphology and movement of the projector apparatus ultimately differed (Figure 1). Chameleons retain a

stationary skeletal element while the accelerator muscle propels itself and the tongue forward. Salamanders, by contrast, anchor the accelerator muscle and launch the skeletal rod along with the tongue. This mirrored configuration reflects their evolutionary history, but both systems prove mechanically equivalent⁶.

The accelerator muscles have just between three and 30 milliseconds and 1–35 mm of travel distance to power the launch of the tongue while squeezing and sliding over the skeletal rod⁶. Given these constraints, the energy they transmit to the movement is exceptional among vertebrates⁶. This is where elastic recoil becomes crucial as a source of power, rather than relying solely on direct muscle contraction⁷. Spirally arranged elastic collagenous tissue is present in both groups^{3,5} (Figure 1). As the muscle hydrostatically elongates during squeezing on the skeletal rod, the spiral orientation of the collagenous fibers will make them store elastic tension to

squeeze³. When the rod's tip reaches a region under such elastic tension, powerful propulsion by elastic recoil of the fibers will be generated. This powerful propulsion continues as the rod tip slides through additional regions of the accelerator muscle under elastic tension. In this way, the tongue accumulates kinetic energy throughout the launch, culminating in its exceptional speed.

Zeng and colleagues⁶ demonstrate that, despite originating from ancestors with a clearly distinct anatomy and method of tongue protrusion, chameleons and lungless salamanders have evolved mechanically equivalent tongue projection systems that maximise speed and reach — a striking example of convergent evolution in a complex biomechanical system.

DECLARATION OF INTERESTS

The author declares no competing interests.

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