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## Short Communications

### A cryptic intermediate in the evolution of chameleon tongue projection

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**Summary.** An incipient form of tongue projection occurs in *Phrynocephalus helioscopus*, a generalized agamid lizard. We argue that this condition represents a functional intermediate between typical lingual prehension and chamaeleontid tongue projection, and that tongue projection evolved in chameleons by augmentation of ancestral mechanisms still operating in related, generalized lizards.

**Key words.** Lizard; Chamaeleontidae; Agamidae; tongue; feeding; evolution.

Chamaeleontid lizards can project their tongues as much as one and a half times their body length. Air<sup>1</sup>, blood<sup>2</sup>, and inertia<sup>3</sup> were proposed alternatively as the agents of lingual projection. Cuvier correctly surmised that muscle contraction imparts the necessary force to the tongue<sup>4</sup>, although his particular interpretation was flawed. We owe our present conception of this mechanism largely to the anatomical inferences of Brücke<sup>5</sup> and subsequent investigators<sup>6–9</sup>.

Despite the attention to and controversy surrounding the mechanism of chameleon tongue projection, the evolution of this singular adaptive complex has been curiously neglected. Our ignorance probably stems from two factors: first, lingual projection is fundamentally a discontinuous process; the tongue is either projected or it is not. In an engineering sense, an intermediate form of tongue projection is difficult to envi-

sion and has never been reported. Second, variation in tongue morphology and function among even generalized lizards has remained largely unexplored<sup>10</sup>. In particular, we lack data on the role of the tongue in feeding, especially its use in prey capture.

In this paper we adduce new functional data demonstrating that an intermediate form of tongue projection exists among extant taxa. We analyze these data in the context of recent phylogenetic hypotheses of squamate relationships and conclude that this functional intermediate represents the retention of an ancestral state linking generalized lizards to chameleons in the evolution of lingual projection.

**Materials and methods.** Phylogenetic conclusions are based on three recent cladistic studies that have established the monophyly of Squamata and the relationships of Iguania,

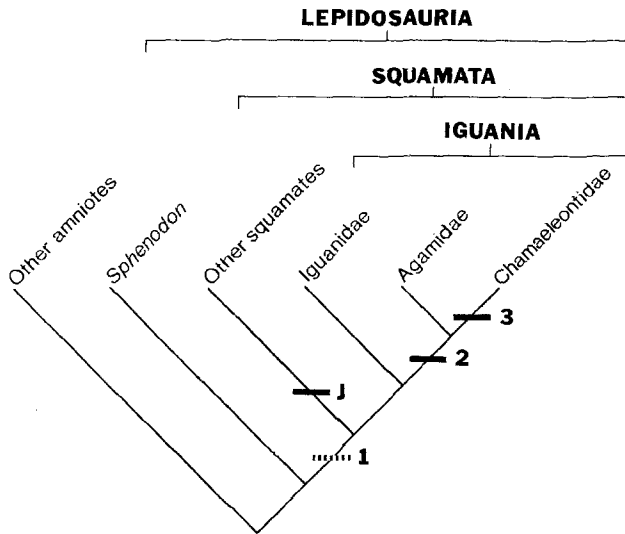


Figure 1. Cladistic relationships among lepidosaurian reptiles based on independent phylogenetic analyses<sup>10-12</sup>. 'Other squamates' refers to all non-iguanian squamates, including snakes and amphisbaenians. The hatched bar indicates the primitive mode of feeding, lingual prehension. The solid bars represent derived states. J = prey prehension with the jaws, a derived condition characterizing all non-iguanian squamates. Character states 1-3 correspond to the three functional-morphological stages identified in the text.

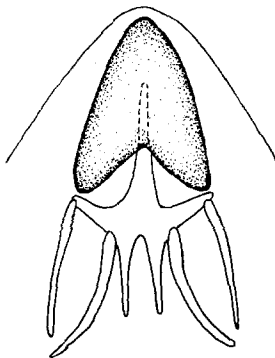


Figure 2. The hyolingual apparatus of a generalized iguanian, *Phrynocephalus helioscopus*, in dorsal view. The dorsal, glandular surface of the tongue is shown in stipple. The entoglossal process of the hyoid (dashed portion) penetrates the muscular body of the tongue. Curved line represents the jaw margin.

within Squamata<sup>10-12</sup>. These studies corroborate earlier conclusions regarding the sister-group relationship of Chamaeleontidae and Agamidae (e.g. Camp<sup>13</sup>) and further show that Squamata comprises two monophyletic lineages, iguanians and non-iguanians (see below). Functional data are drawn from observations of nine living specimens of *Phrynocephalus helioscopus*, a species of Agamidae, and 27 *Chamaeleo zeylanicus* (Chamaeleontidae). Two individuals of *P. helioscopus* feeding on mealworms were filmed at 48 frames per sec with a Bolex 16-mm movie camera and synchronized stroboscopic illumination. Feeding in chameleons was filmed with a Nizo super-8 movie camera at 54 fps in daylight. Chameleons were also photographed with a 35-mm still camera. Figures 3A and B are enlargements of individual 16-mm movie frames. Figure 3C is a 35-mm photograph of a stationary animal. Captive maintenance and natural history data are reported elsewhere<sup>14,15</sup>.

**Results and discussion.** The phylogenetic relationships of Chamaeleontidae are shown in figure 1. A salient feature of the phylogeny is that the cladistic dichotomy between iguanian and non-iguanian squamates represents a functional di-

chotomy as well. Iguanians use their tongues as the organ of prehension during feeding on small food items. In contrast, non-iguanians use their jaws for prey prehension. Use of the tongue during feeding in these species is limited to intraoral food transport. *Sphenodon punctatus* and many non-lepidosaurian amniotes also use their tongues as prehensile organs, therefore lingual prey prehension is inferred to be plesiomorphic (primitive) for squamates<sup>10</sup>. The above observations establish that lingual prey prehension is a primitive behavior retained in all iguanians, not just chameleons, but they do little to mitigate the large gap between lingual feeding in generalized iguanians (agamids, iguanids) and chameleons.

In its simplest sense, the iguanian lingual feeding mechanism comprises a hard skeletal component, the hyoid, and a soft tissue component, the tongue, together forming the hyolingual apparatus (fig. 2). The hyoid is movably suspended in the throat region by a system of strap-like muscles connecting it to the mandible anteriorly and the sternum and shoulder posteriorly. The tongue is complexly muscular and sur-

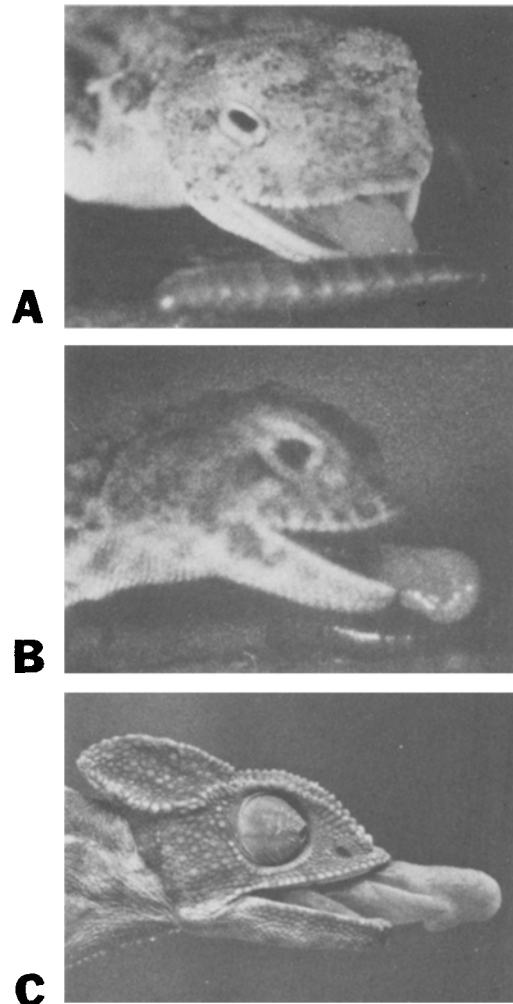


Figure 3. Tongue protrusion in agamid and chamaeleontid lizards. A 'Typical' lingual prey prehension in an agamid, *P. helioscopus*. Note that posterior part of tongue remains in mouth and that only tongue tip is curled ventrally (state 1 in fig. 1). B Maximum tongue protrusion during extreme attempt at prey prehension in *P. helioscopus*. Glandular tongue is protruded beyond mandible and wrapped around muscular shaft supported by entoglossal process (state 2 in fig. 1). C Protrusion ('aiming') stage preceding tongue projection in *C. zeylanicus* (Chamaeleontidae). This conformation (state 2 in fig. 1) is held fixed until projection (state 3). Note its similarity to tongue form of *P. helioscopus* shown in B.

rounds a median, anteriorly directed rod of the hyoid, the entoglossal process, on which it can slide freely. Thus, anterior movement of the tongue (protrusion) can result either from hyoid protraction or lingual translation on the hyoid, or both. The dorsal surface of the tongue is papillose and covered by a simple mucous epithelium. Lingual prey prehension in iguanids and agamids involves orientation of the head toward the prey followed by rapid protrusion of the tongue, contact of the dorsal, lingual surface with the prey item, and retraction of the tongue with adherent prey<sup>16</sup>. This behavior resembles closely that reported for *Sphenodon*<sup>17</sup>. The entire sequence can occur in less than 0.2 s in small species. During protrusion, the back part of the tongue remains within the jaw margin and only the anterior portion curls ventrally to present the dorsal surface toward the prey (fig. 3 A).

In 10 of 24 filmed lingual feeding episodes of *Phrynocephalus helioscopus*, a diminutive agamid species, an extreme form of tongue protrusion was observed (fig. 3 B). In most cases the animal was moving toward its prey (a mealworm) and apparently attempting to span a larger than usual distance with its tongue. In these episodes the dorsal, glandular portion of the tongue (illustrated in fig. 2) was extended beyond the jaw margin and wrapped around the anterior end of a muscular shaft containing the protracted entoglossal process. These extreme protrusions were strikingly different in form from others observed.

In contrast to generalized iguanians, chameleon lingual feeding exhibits four kinematically well-defined stages: sighting, tongue protrusion ('aiming'), projection, and retraction<sup>8, 15</sup>. During aiming, the tongue is cantilevered beyond the jaw margin by protraction of the hyoid (fig. 3 C). The glandular portion of the tongue moves anteroventrally and wraps around the end of the muscular shaft containing the entoglossal process<sup>15</sup>. This conformation is held until projection is initiated some seconds later.

We suggest that the chameleon aiming stage is homologous to the extreme form of tongue protrusion described above for an agamid. As such, these forms of tongue protrusion descended from a common ancestor whose maximum tongue protrusion resembled the condition described here for a living agamid, *P. helioscopus*. This conclusion is supported by two lines of evidence:

1) The agamid and chamaeleontid conformations are remarkably similar in morphology (fig. 3 B, C). In both, the tongue is cantilevered beyond the mandible on the protruded entoglossal process. The tongue musculature has a stout, shaft-like appearance (permanent in chameleons, transiently assumed in the agamid) and the glandular surface is wrapped around its terminus.

2) Chamaeleontidae and Agamidae are sister taxa, i.e. they are each other's nearest phylogenetic relative. Thus, homology of these features is the most parsimonious explanation available in that it requires only a single evolutionary origin for the ability to protrude the tongue in so extreme a manner. This conclusion assumes, of course, that the extreme form of tongue protrusion evident in *P. helioscopus* is characteristic of all agamids, or at least those agamids allied to Chamaeleontidae (the possibility of agamid paraphyly has been raised by several workers<sup>12, 18</sup>).

A third line of indirect support comes from the anatomy of the iguanian tongue and its probable mechanism of protrusion. In both generalized iguanians and chameleons, the entoglossal process is surrounded by a large, intrinsic muscle fiber mass (*M. verticalis* in generalized forms, *M. accelerator linguae* in chameleons)<sup>7, 19, 20</sup>. These muscles are almost certainly homologous (based on topographic identity of the muscles within the tongue), although the accelerator muscle is highly specialized. Its action is to constrict the central lumen containing the entoglossal process, thereby accelerat-

ing the tongue of the process in a manner analogous to squeezing a watermelon seed from between one's fingers<sup>9</sup>. Smith<sup>21</sup> suggested that the verticalis muscle similarly squeezes the entoglossal process in generalized iguanians, thereby causing the tongue to move forward by sliding it along the process. There is as yet no experimental proof of this mechanism in generalized species, but lingual translation during protrusion in generalized and chamaeleontid iguanians could be caused, in part, by a homologous mechanism. The form of tongue protrusion we observed in *P. helioscopus* might be a result of increased verticalis activity, as is lingual projection in chameleons.

The extreme form of tongue protrusion we observed in an agamid lizard represents a functional intermediate between the plesiomorphic condition found in *Sphenodon*, Iguanidae, and Agamidae (most of the time), and the highly derived lingual projection of Chamaeleontidae. In this light, the chamaeleontid mechanism may be viewed as the end result of a three part transformation series<sup>22</sup> (fig. 1): 1) protrusion with hyoid protraction and limited lingual translation caused by extrinsic muscles; little or no activity of verticalis musculature; only tongue tip curls ventrally (the primitive state); 2) additional lingual translation caused by increased verticalis activity; glandular portion of tongue wrapped around end of entoglossal process (first derived state corresponding to extreme protrusion in agamids and the aiming stage of chamaeleontids); 3) forceful action of verticalis (accelerator) musculature resulting in lingual translation off the end of the entoglossal process (second derived state corresponding to chamaeleontid tongue projection).

The transformation series above represents both a possible evolutionary sequence leading to the chamaeleontid projection mechanism and also a kinematic sequence exhibited by an individual chameleon during prey capture. Thus, the kinematic sequence of chameleon tongue projection recapitulates its phylogeny or evolutionary sequence.

We have demonstrated the continuous nature of variation in tongue protrusion among extant iguanians (represented by the three-part transformation series above). Tongue projection is argued to be an extension of mechanisms operating in generalized agamids. This finding supports the general model of tetrapod feeding proposed by Bramble and Wake<sup>23</sup> and underscores their contention that specialized feeding mechanisms, including tongue projection, are outgrowths of generalized, ancestral mechanisms. Ongoing studies are investigating the key functional-morphological innovations in feeding that characterize the chamaeleontid lineage.

An important corollary of this study is its revelation that evolutionarily significant variation may exist in a facultative, temporally brief, and transient form. A functionally transient form would be hidden to investigators using preserved material. Such cryptic variation might, as in this case, represent a key intermediate phenotype that fills an apparent functional and phylogenetic gap. Soft anatomical parts that undergo shape and positional changes, but lack jointed skeletal components that move in predictable ways, are especially suspect. Hyolingual, digestive, circulatory, and hydrostatic structures in general, are likely sources of such cryptic variation among animals and evolutionary morphologists studying these systems should consider their temporally variable nature. Finally, since complex movements of such systems might evolve by accretion of incremental changes, it is conceivable that some kinematic sequences, unlike ontogenetic sequences, recapitulate phylogeny in a true Haeckelian sense.

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## The dopaminergic innervation as observed by immunohistochemistry using anti-dopamine serum in the rat cerebral cortex<sup>1</sup>

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**Summary.** By using an antiserum raised against dopamine bound to bovine serum albumin, thinner dopamine-labeled nerve terminals were visualized immunohistochemically within neocortical areas, in addition to well-documented dopaminergic innervation into the prefrontal and limbic cortices.

**Key words.** Dopamine; cerebral neocortex; immunohistochemistry.

The cortical dopaminergic innervations of the rat was thought for a long time to be localized exclusively within the prefrontal and limbic cortices<sup>2,4,8,9</sup>. However, new dopaminergic terminal fields were recently discovered in some neocortical areas situated along a dorsal sagittal strip, using fluorescence histochemistry after pharmacological manipulation<sup>3</sup>. In the present study, we have reexamined the distribution of cortical dopaminergic innervation, by means of immunohistochemistry using antiserum raised against dopamine in untreated rat brain. Particular emphasis was placed on the investigation of the dopaminergic input into the remaining neocortical areas.

**Materials and methods.** Preparation of antiserum: Production of the antiserum to dopamine (DA) was principally based upon the method of Geffard et al.<sup>5,6</sup>. Briefly, DA hydrochloride (42.4 mg) was coupled to bovine serum albumin (BSA, 40 mg) by adding glutaraldehyde (GA) (0.25 mmol) in 10 ml of 0.1 M phosphate buffer (PB), pH 7.4. While stirring, 1 ml of NaBH<sub>4</sub> (10 mM) was added to the solution. After incubation for 20 min, the solution was dialyzed against PB for 2 days, and centrifuged. The supernatant (0.5 mg/ml protein) was used for immunization. This DA-GA-BSA conjugate was mixed with complete Freund's adjuvant and injected in rabbits at intervals of two weeks. The antiserum was obtained after 4 months.

**Tissue preparation and immunohistochemical staining:** Male Wistar rats weighing 150–400 g were anesthetized with Nembutal and the blood was washed out with about 50 ml of phosphate buffered saline (PBS), and subsequently with 450–900 ml of 5% GA in 0.01 M cacodylate buffer, pH 5–7. After perfusion, the brain was removed and sliced into 3–4-mm thick blocks. After being placed in the same fixative, for 1–3 h, the tissue blocks were sectioned into 40-µm-thick sections on a microslicer (DTK-1000, DSK). These sections were first incubated in 1% NaBH<sub>4</sub> in PBS for

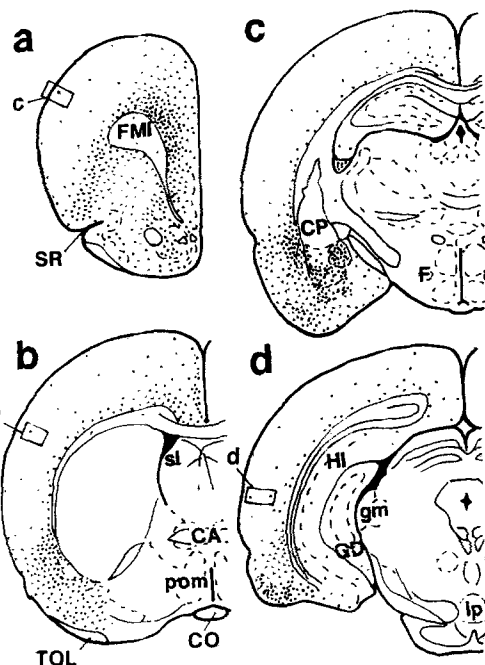


Figure 1. The schematic drawings of dopamine-immunoreactive nerve terminals on frontal sections of the rat cerebral cortex. Note that dense-labeled terminals represented as dots were localized mainly in the prefrontal and limbic cortices, but sparse dopamine-labeled terminals were found throughout the remaining neocortical areas. Rectangles c, d and e indicate the approximate position of the photomicrographs in figure 2. CA, anterior commissure; CO, optic chiasma; CP, nucleus caudatus-putamen; F, fornix; FMI, forceps minor corpus callosum; GD, dentate gyrus; gm, medial geniculate nucleus; HI, hippocampus; ip, interpenduncular nucleus; pom, medial preoptic area; sl, lateral septal nucleus; SR, rhinal sulcus; TOL, lateral olfactory tract.