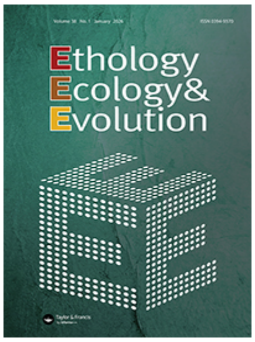

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Ethology Ecology & Evolution

ISSN: 0394-9370 (Print) 1828-7131 (Online) Journal homepage: www.tandfonline.com/journals/teee20

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To cite this article: Aída P. Giozza, Veronica Slobodian, Luisa M. Diele-Viegas, Ricardo S. Magalhães, Marcelle O. Heliópolis & Reuber A. Brandão (04 Jun 2026): Do conspicuous tails and dietary shifts indicate luring behavior in vipers (Serpentes Viperidae)?, Ethology Ecology & Evolution, DOI: 10.1080/03949370.2026.2630806

To link to this article: https://doi.org/10.1080/03949370.2026.2630806

Ethology Ecology & Evolution, 2026
https://doi.org/10.1080/03949370.2026.2630806

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Do conspicuous tails and dietary shifts indicate luring behavior in vipers (Serpentes Viperidae)?

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Received 24 March 2025, accepted 21 November 2025

Aggressive mimicry is an ambush strategy observed in various animal taxa, including snakes, which use caudal luring (CL) to attract prey. CL involves cryptically colored snakes waving a conspicuous tail tip (CTT) to mimic worm-like invertebrates, luring prey that feeds on such organisms. This strategy is common among Viperidae, particularly in juveniles, which often exhibit ontogenetic shifts in diet (OSD) from ectothermic to endothermic prey. Although CL, CTT and OSD are assumed to be correlated, this relationship has never been empirically tested. This study investigated the origin and persistence of CL, CTT and OSD in Viperidae evolution, assessing their phylogenetic signal and testing for correlations. Data on the presence or absence of these traits were compiled from the literature, and phylogenetic comparative methods were used to measure phylogenetic signal, test correlations and reconstruct ancestral character states using parsimony and maximum likelihood. Results revealed strong phylogenetic signals for all three traits and significant correlations between each pair. Maximum likelihood reconstructions suggested that the ancestral Viperidae possessed CL, CTT, and OSD, while parsimony analyses indicated CL and CTT were present in the ancestor, but OSD was not. These findings support the hypothesis that CL, CTT and OSD are evolutionarily linked and have been integral to Viperidae since their origin. Despite being the most comprehensive study on these traits, significant gaps in viper natural history data were identified. This highlights the need for further descriptive ecological studies to enhance understanding of viperid biology and support broader macroevolutionary research.

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KEY WORDS: ancestral character reconstruction, caudal luring, evolution, ontogenetic shifts in diet, phylogenetic comparative methods, *Bothrops*, *Crotalus*, *Vipera*.

INTRODUCTION

Predators across the animal kingdom exhibit a wide range of strategies to hunt and capture prey (Glaudas & Alexander 2017). One such strategy is aggressive mimicry, where predators deceive their prey by resembling something neutral, beneficial or even the prey itself (Greene 1997; Ramya et al. 2017). This form of mimicry entices prey through misleading signals, facilitating capture (Glaudas & Alexander 2017).

A particularly intriguing case of aggressive mimicry occurs when predators imitate prey food items. For example, the alligator snapping turtle possesses an annelid-like tongue projection that attracts fish (Harrel & Stringer 1997), while some spiders weave webs mimicking the visual cues of their prey's food (Jackson 1992; Ramya et al. 2017). This strategy spans several animal taxa, from invertebrates (Jackson 1992; Marshall & Hill 2009; Wignall & Taylor 2011; Ramya et al. 2017) to vertebrates (Atkinson 1997; Harrel & Stringer 1997).

Among vertebrates, snakes exhibit an especially fascinating form of aggressive mimicry known as caudal luring. As strictly carnivorous animals (Marques et al. 2019), snakes employ various foraging strategies, ranging from active searching to ambush predation (Lillywhite 2014). Some ambush-hunting snakes use lingual luring, a behavior where tongue flicks on the water's surface mimic insect wing movements — observed in species like *Nerodia clarkii* (Baird & Girard 1853), *N. rhombifer* (Hallowell 1852), *N. sipedon* (Linnaeus 1758) and *Thamnophis atratus* Kennicot 1860, the dipsadid *Mesotes strigatus* (Günther 1858) and the viperid *Bitis arietans* (Merrem 1820) (Mario-da-Rosa et al. 2020).

Even more widespread than lingual luring is caudal luring (CL), where cryptically-colored snakes attract prey by wriggling a conspicuous, worm-like tail tip (Heatwole & Davison 1976; Reiserer & Schuett 2008). Tail movement and conspicuous coloration patterns are significant traits that have shaped the morphology of viperid tail tips to resemble various invertebrate taxa, which is essential for caudal luring to be effective (Heatwole & Davison 1976; Reiserer 2002; Reiserer & Schuett 2008). This behavior allows ambush-hunting snakes to actively lure prey without expending energy chasing them, thus also reducing exposure to predators (Reiserer 2002). Caudal luring has been reported in species across various families — including *Tropidodryas striaticeps* (Cope 1870), *Pantherophis alleghaniensis* (Holbrook 1836), *Boa constrictor* Linnaeus 1758 (Boidae), *Morelia viridis* (Schlegel 1872) (Pythonidae), *Acanthophis antarcticus* (Shaw 1802) and *Acanthophis praelongus* Ramsay 1877 (Elapidae) (Murphy et al. 1978; Radcliffe et al. 1980; Chiszar et al. 1990; Sazima & Puorto 1993; Mullin 1999; Hagman et al. 2008) — but is particularly common in the ambush-hunting Viperidae family (Reiserer & Schuett 2008).

Viperidae comprises 365 species across 35 genera, within the subfamilies Azemiopinae, Crotalinae and Viperinae (Uetz et al. 2026). Most CL reports involve juvenile crotalines, including species like *Agkistrodon contortrix* (Linnaeus 1766), *A. piscivorus* (Lacépède 1789), *A. bilineatus* Günther 1863, *Hypnale hypnale* (Merrem 1820) and *Metlapilcoatlus nummifer* (Rüppell 1845) (Neill 1960; Heatwole & Davison 1976). The behavior is thought to occur under two conditions: (1) the snake is cryptic against the environment, with only its tail tip visible; and (2) visible prey is nearby (Neill 1948, 1960). Nonetheless, direct observations of CL remain scarce, and many inferences rely on the assumption that a conspicuous tail tip indicates this behavior (Heatwole & Davison 1976; da Fonseca et al. 2019).

It is also commonly suggested that only juveniles perform CL, as adults often lose their distinctive tail coloration, rendering the tail visually similar to the rest of the body (Heatwole & Davison 1976). This has led to the hypothesis that CL is associated with conspicuous tail tips (e.g. Neill 1960; Martins et al. 2002; Del Marmol et al. 2016) and disappears in adulthood due to ontogenetic shifts in diet (OSD) — a transition from ectothermic to endothermic prey (Greene & Campbell 1972; Heatwole & Davison 1976). However, some adult snakes, such as *Bothrops bilineatus* (Wied-Neuwied 1821), *B. insularis* (Amaral 1922) and *Cerastes vipera* (Linneaus 1758), retain both their conspicuous tails and CL behavior, possibly due to the absence of OSD (Greene & Campbell 1972; Heatwole & Davison 1976).

The brightly colored tail is present in various snake species from different families and might have different functions than caudal luring (Greene 1973), the primary behavior investigated in this work. There are several examples of tail display in snakes, and various possible explanations for it, other than the attraction of prey. These include acting as a decoy, to divert attack to the tail; warning the predator of the snake's venomous bite (aposematic displays), which may lead to Batesian mimicry from harmless species; disorienting a predator with a "flash display", increasing the snake's time to flee while its predator is disoriented; pseudoautotomy (breaking the tail off without regeneration) as a defense strategy; and it may have no recognized function at all (Greene 1973; Costa et al. 2014).

Despite frequent mention in the literature, no study has comprehensively examined the evolutionary pattern of caudal luring across Viperidae or its correlation with conspicuous tail tips and dietary shifts. Therefore, this study investigates how caudal luring evolved in vipers. Specifically, we test the hypothesis that caudal luring, conspicuous tail tips, and ontogenetic shifts in diet are evolutionarily correlated in Viperidae. We predict that viperid lineages exhibiting caudal luring also possess conspicuous tail tips and shift their diet from ectothermic to endothermic prey during development.

MATERIALS AND METHODS

Study group

We searched for information on all viperid species presented in the Viperidae phylogeny of Alencar et al. (2016). This phylogeny is currently the most comprehensive phylogenetic hypothesis for the family, with 263 from the 365 species known at the time of the analyses (Uetz et al. 2026), distributed in 34 of the 35 Viperidae genera[1]. We also included 25 species present in the Alencar et al. (2016) phylogeny as outgroups belonging to the families Xenodermidae, Acrochordidae, Pareidae, Pseudoxyrhophiidae, Elapidae, Colubridae and Homalopsidae for the comparative analyses. We collected, for every species, data on the presence or absence of three binary characters: caudal luring (CL), the ontogenetic shift in diet (OSD) and conspicuous tail tip (CTT). We will detail the data collection procedure further below.

Data collection

We searched systematically in the scientific literature for information regarding the presence or absence of caudal luring (CL), ontogenetic shift in diet (OSD) and conspicuous tail tip (CTT). The searched keywords were the species' scientific name and/or its common names combined with character keywords (behavior, diet, caudal luring, feeding behavior, juvenile, ecology, natural history). We conducted the search mainly in English, but also in Portuguese, Spanish and French, besides other languages according to the species' countries of occurrence.

We gathered information available primarily on published scientific papers, life-history books and field guides, complemented with evidence obtained from online databases (e.g. Reptile Database), citizen science and scientific popularization websites (e.g. iNaturalist) in which the information was referenced to scientific literature. The mentioned websites were the source of information regarding the presence of conspicuous tail tips for species where scientific literature was scarce. Nevertheless, we only used pictures that presented reliable species identification (made by specialists and/or with properly cited references). When a reliable species identification was not found at the source of the image, we contacted the author to verify how the snake was identified or contacted group specialists to confirm its identification.

The data for the presence or absence of CL, OSD and CTT was assembled in a discrete data matrix (see Supplemental Data), coding the presence (Yes) or absence (No) as binary characters. The data matrix presents Viperidae species for which information was found about at least one of the three characters.

A massive effort was made to separate conjectural from actual evidence about the characters of interest. On caudal luring, we disregarded mere assumptions and suppositions made concerning the presence of this behavior in a given species (e.g. Neill 1960; Martins et al. 2002; Del Marmol et al. 2016), taking into consideration only information from studies about the natural history or where the behavior was recorded and described, as well as direct observations (videos, personal communication with authors) that reported caudal luring. We only considered ontogenetic shifts in diet from eating mainly ectothermic prey when juveniles to eating mainly endothermic prey while adults (therefore, we did not include studies that did not specify clearly which prey was captured by adults and those captured by juveniles). We considered as a conspicuous tail tip any tail whose coloration and/or shape was remarkably different from the snake's body. Regarding rattlesnakes, we did not consider the rattle as conspicuous per se, only when the coloration of the tail itself was different from the remaining body.

Ancestral character reconstruction and evolutionary models

To understand how CL, OSD and CTT evolved in vipers, we used two methods of character optimization and ancestral reconstruction for each character: a parsimony and a likelihood approach. Under the parsimony paradigm, the Fitch parsimony algorithm (Fitch 1971), with accelerated transformation optimization (ACCTRAN), as suggested by de Pinna (1991), was conducted on Winclada software (Nixon 2002) for ancestral character reconstruction and optimization. Using Fitch's parsimony algorithm (Fitch 1971), we can find out the number of character state transitions, as well as the ancestral character states in each node of the phylogenetic tree while considering uncertainties related to missing information about one or two of the three traits studied while reconstructing the ancestral states of the characters. In the context of comparative methods, parsimony analyses are important because they allow us to include taxa with missing information in the search for the most parsimonious scenario of character evolution. However, parsimony methods have a different ontology than likelihood methods, being thus not comparable and not bringing statistical information along with the results.

Besides parsimony reconstruction, a maximum likelihood approach was conducted in a reduced matrix and pruned tree to include only species with complete information regarding each of the three characters. A maximum likelihood (ML) ancestral character state reconstruction was performed using R (R Core Team 2019), via RStudio (Team R 2019). To perform the ancestral character reconstruction, we tested different models for state transition rates, using the *fitDiscrete* function of the "geiger" R-package (Harmon et al. 2008), under a Pagel's lambda transformation (see more in the next section), and we opted for the model with the lowest scores for AICc and log-likelihood, using a chi-squared ratio test (Carvajal-Castro et al. 2020). We tested the "Equal Rates model" (ER) as well as the "All-Rates Different model" (ARD), the first assuming that all transitions between trait states occur at the same rate (Pagel 1994; Lewis 2001) and the latter assuming that all transitions occur at different rates (Paradis et al. 2004).

The character reconstructions were performed with the best-fitted model for each character, using the *ace* function of the R-package "ape" (v. 5.3; Paradis & Schliep 2018). This function estimates the ancestral states of the characters studied employing maximum likelihood (in case of discrete characters), as well as the associated uncertainty (Paradis & Schliep 2018). The likelihood values were calculated with a joint estimation procedure (further discussed at Felsenstein 2004), which is faster than stochastic mapping while being similarly accurate (Paradis & Schliep 2018). The results were plotted in the trimmed tree via the *plotTree* function of "phytools" (v. 0.7.20; Revell 2012) R-package, with the posterior probability values at the nodes. Figures were edited using Adobe Illustrator 2019.

Phylogenetic signal

We measured the phylogenetic signal to assess the measurement of non-independence among species trait values (caudal luring, ontogenetic shift in diet and conspicuous tail tips) because of their phylogenetic relatedness (Felsenstein 1985). We used Pagel's statistic lambda (λ) (Pagel 1997, 1999), which assumes a Brownian motion model of trait evolution, and with indices close to zero indicating phylogenetic independence for that trait, while values close to one indicate the trait is distributed as expected under a Brownian motion evolutionary model (Pagel 1999). We chose Pagel's λ because it is less susceptible to the number of analyzed species (Münkemüller et al. 2012) and can be implemented for discrete binary datasets. The phylogenetic signal was measured for each character within the best-fitted model for state transition rates in R, with the *fitDiscrete* function of the "geiger" R-package.

Correlation analyses between discrete traits

To measure the strength of the correlation between caudal luring, ontogenetic shifts in diet and conspicuous tail tips, given the phylogenetic relationships of Viperidae species, we performed a Pagel's fitting test (Pagel 1994) using the *fitPagel* function of the "phytools" R-package. This test measures the likelihood of correlated evolution between two binary characters, given the phylogenetic trees' branch lengths and best-fitted model for state transition rates. We ran the *fitPagel* function for the investigated characters arranged in pairs (CL-CTT, CL-OSD and OSD-CTT), using a reduced matrix with complete data for both characters and the previously obtained model for the characters' evolution (ER or ARD). When the two analyzed traits had different best-fitted models, we chose the most complex model (ARD) to run the analyses, since one of the traits was not well-explained by the simplest model (ER).

RESULTS

From the 263 Viperidae species investigated, we found information regarding at least one character (CL, OSD and/or CTT) for 220 species (60.3% of all Viperidae species, 83.7% of the species included in Alencar et al. 2016), as well as for 20 of the 25 species included as the outgroup, resulting in 240 species in total (Fig. 1). From the

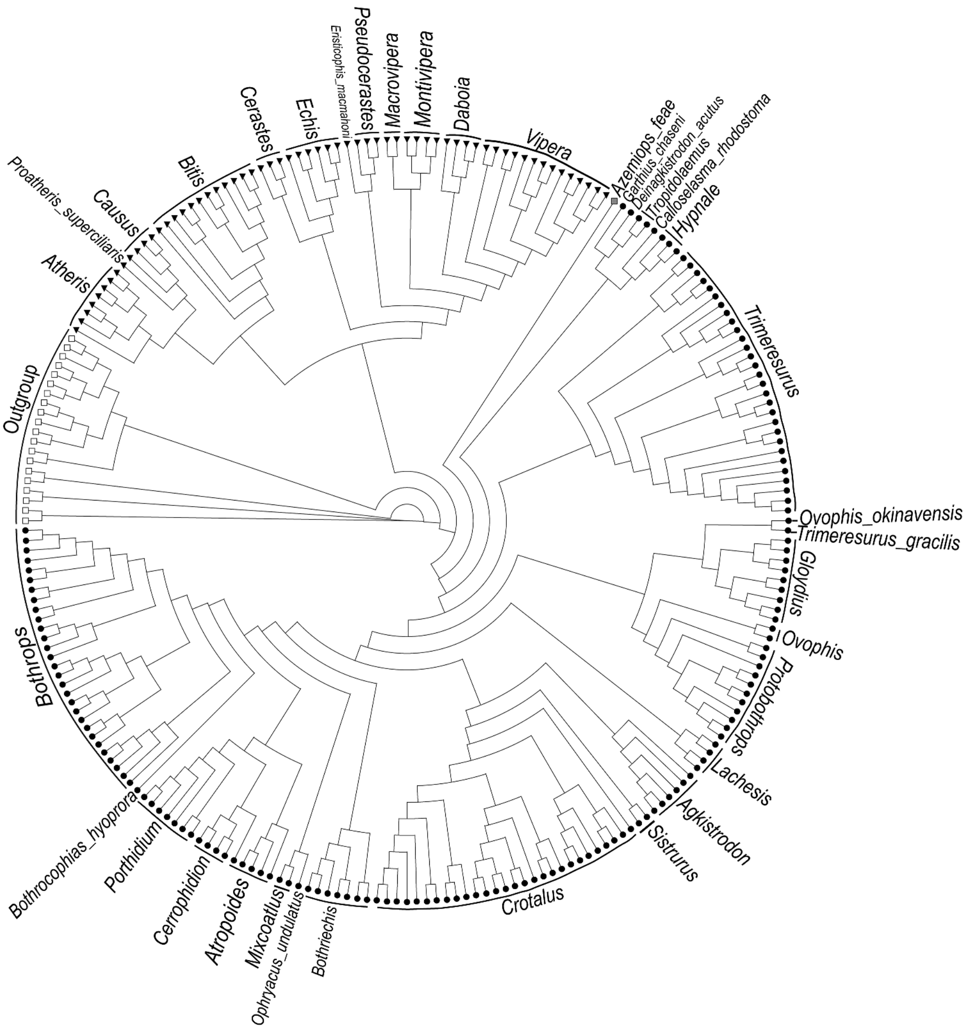

Fig. 1. — The phylogenetic tree for the 240 species of Viperidae, taken from Alencar et al. 2016, analyzed herein. Black circles: Crotalinae species. Black triangles: Viperinae species. Grey square: Azemiopinae species. White squares: outgroup species.

220 Viperidae species, 78 (21.4% of all Viperidae, 29.7% of Alencar et al. 2016 tree) had available information about caudal luring (48 "Yes" and 30 "No"), 163 (44.7% of all Viperidae, 62.0% of Alencar et al. 2016 tree) about ontogenetic shift in diet (88 "Yes" and 75 "No") and 212 (58.1% of all Viperidae, 80.6% of Alencar et al. 2016 tree) about conspicuous tail tip (163 "Yes" and 49 "No"). Only 62 (17.0% of all Viperidae, 23.6% of Alencar et al. 2016 tree) species have available information for all three characters. Most of the information is regarding Crotalinae species, adding up to 157 species (71.4% of our matrix), while only 62 species (28.2% of our matrix) are from the Viperinae subfamily. We also found information on one of the two species of

Azemiopinae known at the time. For more detailed information, see Table S1 in Supplemental Data.

Parsimony reconstruction

The parsimony reconstructions for the entire dataset (240 species), with ACCTRAN optimization, suggest that the Viperidae ancestor presented caudal luring behavior (CL) and conspicuous tail tip (CTT), but no ontogenetic shift in diet (OSD) (Fig. 2). The results of these reconstructions in detail are found in Figs A1-A3 in Supplemental Data. Both CL and CTT are present at the Viperidae origin and were subsequently lost at some points, while OSD appeared at least 19 independent times. Furthermore, the ancestors of each of the three subfamilies (Viperinae, Azemiopinae and Crotalinae) possessed CL and CTT, but not OSD.

The parsimony reconstruction also points out that, despite the CL originating in the Viperidae ancestor, it was lost at least 10 times during the Viperidae evolution and reappeared at least four times. However, we do not have information regarding CL for a great number of species.

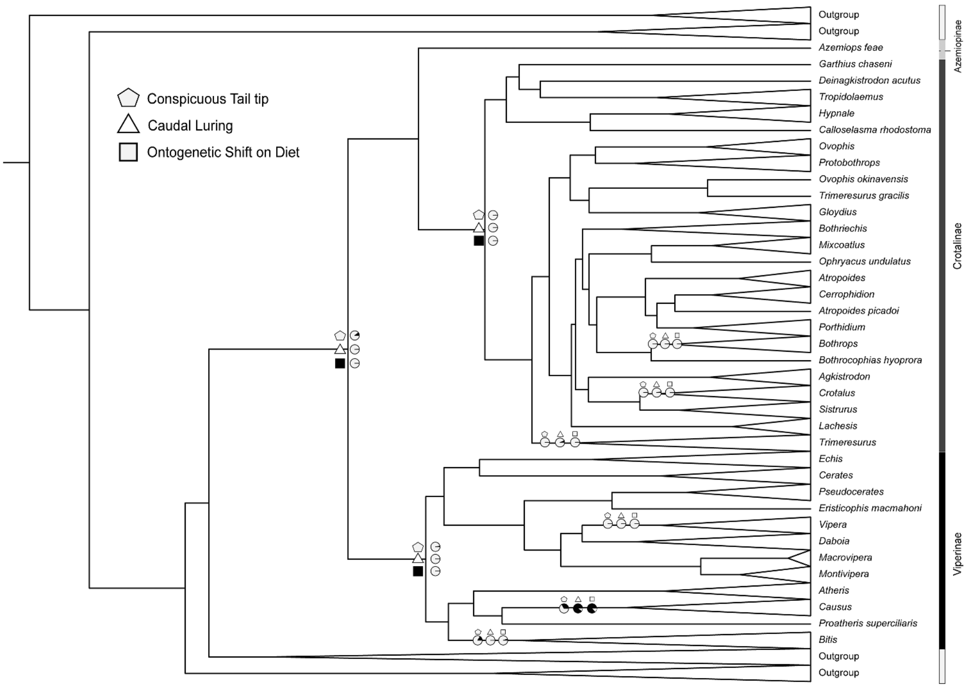

Fig. 2. — Phylogeny of Viperidae genera, with results extracted from Maximum Likelihood (ML) analyses illustrated by the pie-charts and Parsimony analyses by square, triangle and pentagon. White means the character was present and black means character absent. Triangle: caudal luring (CL). Pentagon: conspicuous tail tip (CTT). Square: ontogenetic shifts on diet (OSD). For information in species-level detail, see Figs S1-S6 in Supplemental Data.

As for CTT, even though the character was lost at least 26 times in some lineages, and secondarily gained only five times, this character was widely sampled and is present in most species of the family. Finally, regarding OSD, despite not being present in the ancestor of Viperidae nor in the ancestors of the subfamilies, it appeared at the base of some diverse clades, with the New World Crotalinae (minus the genus *Lachesis*) being the most remarkable one.

Maximum likelihood reconstruction

The maximum likelihood (ML) ancestral state reconstructions were made with the reduced datasets for which we had information regarding at least one of the characters (78 species for caudal luring, 163 species for ontogenetic shifts in diet and 212 species for conspicuous tail tips). The results of these reconstructions in detail are found in Figs A4-A6 in Supplemental Data. Both CL and OSD reconstructions were made under the ARD model for state transition rates, which presented the lower Akaike values (CL: AICc = 93.291; OSD: AICc = 185.825), while the CTT reconstruction was made under the ER model (AICc = 213.619). All three analyzed characters showed a strong phylogenetic signal, statistically different from zero (caudal luring $\lambda = 0.850$, $P = 0.001$; ontogenetic shift in diet $\lambda = 0.874$, $P = 0.002$; and conspicuous tail tips $\lambda = 0.874$, $P = 0.012$).

The ML analyses indicated a high probability of the ancestor of the Viperidae family presenting CL, OSD and CTT, as well as the ancestors of the Viperinae and Crotalinae subfamilies (Fig. 2). As for the Azemiopinae, we only had information about conspicuous tail tips, that are absent in its members but are probably present in the ancestor of Azemiopinae + Crotalinae. Further, the ML analyses also indicate that CL was lost at least 13 times along viperid evolution, CTT was lost 24 times, and OSD was lost 33 times after its first appearance.

Correlation analyses

The complete data matrix for caudal luring and conspicuous tail tip has 72 species. The matrix for caudal luring and ontogenetic shift in diet has 68 species, and the matrix for conspicuous tail tips and ontogenetic shifts in diet has 128 species. All three pairs of characters were tested for correlation under the ARD model. The tests showed that the dependent model matrix explains the evolution of all three pairs of characters significantly better than the independent model, meaning that these characters likely evolved correlatedly (Table 1).

DISCUSSION

Snakes are quite different from other vertebrates because of morphological, behavioral and ecological constraints imposed by the lack of limbs (Greene 1997; Lillywhite 2014). Nevertheless, the group shows an astonishing diversity and the development of several foraging strategies, including specialized hunting tactics for prey approaching and capturing (Vitt & Caldwell 2014; Title et al. 2024). One of the most striking of these strategies is the use of caudal luring, which is largely present in

Table 1.

Scores of the dependent and independent rate matrix models of the correlation tests, for each pair of characters. "CL vs CTT": caudal luring and conspicuous tail tips. "CL vs OSD": caudal luring and ontogenetic shift in diet. "CTT vs OSD": conspicuous tail tips and ontogenetic shift in diet.

	CL vs CTT		CL vs OSD		CTT vs OSD	
	Dependent model	Independent model	Dependent model	Independent model	Dependent model	Independent model
Log-likelihood	– 65.081	– 86.064	– 66.527	– 83.352	– 141.338	– 148.969
Likelihood-ratio	41.964		33.65		15.262	
P-value	0.014		<< 0.001		0.004	

the Viperidae family (Reiserer & Schuett 2008), despite natural history reports on caudal luring being somewhat scarce in literature. Herein, we suggest that the presence of caudal luring is congruent with Viperidae evolution and strongly related to the presence of conspicuous tail tip and ontogenetic shift in the snakes' diet, from ectothermic to endothermic prey. It is worth remarking that, in the present study, we considered only the presence or absence of the characters CTT, CL and OSD, without accounting for other factors that may influence the evolution of these traits, such as body and head size.

Even though Parsimony and Maximum Likelihood have different ontologies and, therefore, are not directly comparable, both of these analyses presented very similar results. Our results (for both parsimony and likelihood analyses) proposed that caudal luring evolved early in the phylogenetic history of Viperidae, being present in its ancestor. Also, the parsimony reconstruction indicated that many viperid species for which we do not have CL data might present it as one of their foraging strategies. It has been suggested that caudal luring happens in response to hunger and/or to the presence of prey, misleading the prey into attacking the snake's tail (Greene & Campbell 1972). As observed by Hagman et al. (2008), caudal luring is induced by the approach of suitable prey and increases the number of opportunities to capture prey. The improvement in prey capture opportunities might have led to a positive selective pressure, maintaining caudal luring in many Viperidae species along their evolution. The homoplastic presence of this strategy in several snake families with no recent common ancestor is putative evidence of caudal luring effectiveness for different prey types. Also, the context in which caudal luring is performed by the snake is important, since some prey would never respond to the luring, while some are likely to react to the lure under various conditions (Hagman et al. 2008).

It has been suggested that snakes that display caudal luring were subjected to selective pressures leading to matching cryptically-colored body and different-colored, conspicuous tail tip (Farrell et al. 2011). These selective pressures might be due to the beneficial effect that even a small growth in foraging success due to conspicuous tail tips has in juvenile snakes. Since most caudal luring snakes lose their conspicuous tail following the first year of their life, any addition of prey in that initial year might be crucial to determine the individual's survival and, therefore, the positive selection of these characters (Farrell et al. 2011). Furthermore, this selective advantage might have led to a coloration and movement sophistication that made the tail even more similar to the prey item of the lured species while visually dissociating the tail from the cryptic snake's body (Heatwole & Davison 1976). That level of morphology and movement specialization can be explicitly seen in the tail of *Pseudocerastes urarachnoides*.

However, when there are no indications of such pressures, the luring motion of the tail tip was suggested as more important to the presence of caudal luring than its color. One example is the pigmy rattlesnake, *Sistrurus miliarius* (Linnaeus 1766), a viperid with a cryptic colored body, having a slightly different tail tip, but with caudal luring behavior (Farrell et al. 2011).

According to the results, conspicuous tail tips arose early in Viperidae evolution and are present in most species. However, even though we can observe correlations between form and function in these characters, it is challenging to find strong evidence of empirical causation for them (Hagman et al. 2008). Nevertheless, the matching presence (or the lack of it) of caudal luring and conspicuous tail tips leads to a discussion regarding CTT evolutionary origin and its persistence.

Conspicuous tail tips are found in several snake families, which means there can possibly be different functions other than caudal (Greene 1973). As discussed before, tail displays can have many different explanations without relation to caudal luring, such as flash displays, aposematic signaling, pseudoautotomy, etc. (Greene 1973; Costa et al. 2014). Red is frequently used in aposematic displays. Species of the *Trimeresurus* genus often have a reddish coloration on their tail (see Supplemental Data). Tail display has been observed in stress situations on *Trimeresurus gramineus* (Shaw 1802) (sensu Alencar et al. 2016) when individuals thrash the tail from side to side, but the tail movement was never seen in response to prey (Greene & Campbell 1972). Such movements might relate to a flash or defensive display.

Rattlesnakes (*Crotalus*) form an important group with conspicuous tail tips. Out of 28 investigated species of rattlesnakes, there are 16 with conspicuous tail tips (57%), with various rattlesnake species possessing black and white bandings on their tail, which is thought to be aposematic signaling (Reiserer & Schuett 2016). The relationship between CTT and the other two characters in rattlesnakes will be further discussed later in this paper.

As mentioned earlier, tail movement and patterns of conspicuous coloration are significant traits that have shaped the morphology of viperid tail tips to resemble various invertebrate taxa, which is essential for caudal luring to be effective. Therefore, the presence of conspicuous tail tips that do not mimic invertebrates might be correlated with the absence of caudal luring in these species (e.g. *Crotalus atrox* Baird & Girard 1853, *Crotalus ruber* Cope 1892, *Trimeresurus insularis* Kramer 1977).

Accordingly, the presence of a conspicuous tail tip seems essential to the display of caudal luring behavior since its resemblance to worm-like invertebrates, along with tail movement, is what attracts the snake's prey (Heatwole & Davison 1976; Reiserer & Schuett 2008). Due to the presence of a conspicuous tail tip in most *Bothrops* species, caudal luring has often been inferred for this genus (Lira-da-Silva 2009; Andrade et al. 2010; Carrasco et al. 2010; Valencia et al. 2016). In our work, 13 out of 29 (44.82%; 10 with missing information) species of the *Bothrops* genus present caudal luring, while the majority (86.2%, no missing information) have conspicuous tail tips. Even though the basalmost clade of *Bothrops* (*B. alternatus* group sensu Fenwick et al. 2009) does not present caudal luring, and two out of the five species do not present conspicuous tail tips, our analyses suggest both characters were present early in *Bothrops* evolution. These results corroborate the suggestions made throughout the literature (see above). However, the natural history of the species, from which caudal luring is inferred, should be further investigated to confirm its presence.

In this work, we found that all viperid species showing caudal luring also have conspicuous tail tips, except for *Bitis arietans*. However, the reverse apparently is not true, since we found that the presence of a conspicuous tail tip does not necessarily mean that species also present caudal luring, differently than what was previously suggested (Neill 1960).

Despite presenting caudal luring, lingual luring (attraction of prey by movements of the snake's tongue) is more efficient in the attraction of prey in puff adders (*B. arietans*) than caudal luring (Glaudas & Alexander 2017). The differences in the efficiency of both types of luring might be related to the presence of a contrasting-colored tongue compared to the head. Meanwhile, this snake has a uniform coloration on its tail and body (Glaudas & Alexander 2017).

Also, among the species that present conspicuous tail tips but are not known to caudal lure, we can highlight *Causus lichtensteinii* (Jan 1859), *Trimeresurus insularis*, *Lachesis muta*, *Crotalus horridus*, *Bothrops fonsecai* Hoge & Belluomini 1959, *B. itapetiningae* (Boulenger 1907) and *B. diporus* Cope 1862. At least three of these species' tail tips, although conspicuous, are not mimetic signals and, consequently, not eligible for caudal lure (*Trimeresurus insularis*, *Lachesis muta* and *Crotalus horridus*). Although *Causus lichtensteinii* possesses a conspicuous tail tip, it is an active forager (Coimbra et al. 2018), which contradicts the core principle of caudal luring — an essentially ambush-based strategy. Moreover, the conspicuous tail tip has been lost in its congeners, suggesting that its presence in *C. lichtensteinii* may represent the retention of a plesiomorphic trait. Additionally, it remains possible that the CTT in this species serves an as-yet unidentified function. Nevertheless, nearly all of these species (with the exception of *T. insularis*, for which data are lacking) do not exhibit ontogenetic dietary shifts, reinforcing the proposed correlation between this trait and caudal luring. Notably, the absence of reported luring in some species does not preclude its occurrence — environmental context or observational limitations (e.g. rare or natural-setting behaviors) may explain gaps in documentation.

According to the ML results, an ontogenetic shift in diet is an ancestral character of the family Viperidae. However, parsimony results did not conclude the same and indicated ontogenetic shifts in diet within a scenario of at least 19 independent emergences along Viperidae evolution. Even though the different methods returned different results regarding OSD evolution, we should still take into consideration both hypotheses, since parsimony analysis allows the inclusion of taxa with missing information in the search for the most parsimonious scenario of character evolution, while ML analysis gives us the probability of the existence of a character evolution scenario using only taxa with complete information regarding the characters studied.

Ontogenetic shifts in diet might occur due to many differences between young and adult snakes regarding physiology, morphology and behavior (Mushinsky 1987, apud; Andrade & Abe 1999). The variety of prey that a snake can eat is limited by the gape of the mouth and, generally, the newborn snakes are too small to swallow the same prey as the adults (Girons 1980; Lillywhite 2014). Therefore, as the snake grows, the variety of prey types it can eat increases (Girons 1980). It has been suggested that the ontogenetic shift in diet is related to competition avoidance between young and adult snakes, which might lead to a strong selective pressure toward ontogenetic shifts in diet (Girons 1980), but studies on more viperids should be conducted to test this hypothesis for the family.

In our results, most of the species that present caudal luring also have ontogenetic shifts in diet (64.58%). However, some species do not change the type of prey as they grow, such as *Bitis peringueyi* (Boulenger 1888), *Bitis schneideri* (Boettger 1886), *Bitis caudalis* (Smith 1839) and *Cerastes vipera*, despite presenting caudal luring. Even though there is no ontogenetic shift in diet, these species continue to eat ectothermic prey as adults. Also, they are relatively small after reaching full size (Heatwole & Davison 1976; Shine et al. 1998; Reiserer & DeNardo 2000; Maritz & Alexander 2014). Therefore, caudal luring might be present throughout the entire life of these species, targeting the same type of prey.

Only a few species of the *Trimeresurus* genus had available information about caudal luring and ontogenetic shifts in diet (two and seven, respectively, of 30 species in total). Meanwhile, we found information on conspicuous tail tips for all its species. Even though there is limited natural history information available for this group, our findings revealed that, despite presenting a conspicuous tail tip, *T. insularis* does not present caudal luring.

Rattlesnakes comprise both *Sistrurus* and *Crotalus* genera, and the ancestor of this clade has a high probability of presenting caudal luring, conspicuous tail tips and ontogenetic shifts in diet. The evolution of the three characters in this clade appears to be more complicated to explain. The two *Sistrurus* species analysed herein present all three characters. Regarding the *Crotalus* clade, 16 out of the 28 species investigated for conspicuous tail tips present the character; meanwhile, from the eight species with information regarding caudal luring, only three present the behavior. In this sense, our Parsimony and ML reconstructions suggest very different scenarios for caudal luring evolution in *Crotalus*: despite ML indicating a high probability of the ancestor presenting the behavior, Parsimony indicates the ancestor of *Crotalus* did not caudal lure and the behavior was regained at least three times in the genus.

However, even though further research is necessary to better understand caudal luring evolution in *Crotalus*, natural history might indicate cues for the presence of caudal luring in species for which it was never recorded. This is the case for *C. enyo* (Cope 1861), *C. ravus* Cope 1865, *C. aquilus* Klauber 1952 and *C. triseriatus* (Wagler 1830), whose ancestors might have caudal luring according to Parsimony reconstruction, despite the missing information. These species are all relatively small, never exceeding 80 cm in mean size, making them similar to species that use caudal luring, such as *C. lepidus* (Kennicott 1861), *C. cerastes* Hallowell 1854 and *C. willardi* Meek 1905.

Also, regarding rattlesnakes, the most recently diverged species (*Crotalus ruber* group sensu Douglas et al. 2006) lack caudal luring, while presenting conspicuous tail tips with elaborate warning signals used as aposematic displays. As mentioned above, various rattlesnake species possess black and white bandings on their tail (Reiserer et al. 2016), however, those bright markings are not present in most basal species of rattlesnakes, such as *C. pricei* Van Denburgh 1895, *C. aquilus* Klauber 1952, *C. ravus* Cope 1865 and *C. polystictus* (Cope 1865), which present larvae-like tail tips. It has been suggested that caudal luring and mimicry had a key role in the evolution of the rattle and that there was a transition from the larvae-like tail tip to warning signals that comprise elaborate aposematic displays, including black and white markings on the tail and loud rattling sounds (Reiserer & Schuett 2016).

Thus, to better understand caudal luring evolution in rattlesnakes, the type of prey consumed by the species must also be taken into consideration. From the three (out of eight) *Crotalus* species that caudal lure, *C. cerates* and *C. willardi* also present ontogenetic shifts in diet, while *C. lepidus* eats mainly ectothermic prey during all stages of its life. In sum, while substantial data exist for *Crotalus* (e.g. their well-documented diets), a more complete understanding of caudal luring evolution in rattlesnakes requires integrating this knowledge with detailed natural history observations across a broader range of species.

Finally, we found that all three analyzed characters present a strong phylogenetic signal. This shows that caudal luring, conspicuous tail tips, and ontogenetic shift in diet are conserved characters along the phylogeny, evolving according to the species relations (phylogenetic dependence). Therefore, the maintenance of these characters on extant species is not necessarily related to selective pressures currently acting on them (Farrell et al. 2011), and even past environmental pressures relevant to the emergence and permanence of those characters can only be discussed regarding larger clades (such as we did with the rattlesnakes).

Accordingly, most changes in character states happened in the common ancestors of clades with one or more genera and were maintained along their evolution, most of the time with only a few specific reversions. Thus, it indicates that the retention of ancestral states over time (phylogenetic conservatism) is a significant characteristic of caudal luring, conspicuous tail tip and ontogenetic shifts in diet along viperid evolution. In particular, conspicuous tail tips are present in virtually all viperid groups, with only a few species in each group having lost this character.

Despite having found information about most of the species studied regarding the presence or absence of at least one of the three characters (CL, CTT and OSD), there is still a significant lack of information about the natural history of many species. Most studies involving viperids focus on their venom and its pharmacological and epidemiological aspects. The majority of information gaps pertained to caudal luring and ontogenetic shifts in diet, both of which are behavioral traits. Despite these substantial gaps in literature, which could potentially reduce the confidence in the results presented in this work, we believe we have made significant advances in understanding the evolution of these characters.

CONCLUSIONS

The relationships between caudal luring and conspicuous tail tips (especially those that mimic invertebrate larvae), as well as between caudal luring and ontogenetic shifts in diet, have been suggested throughout scientific literature but have never been tested up to this date. In this study, we gathered information on 220 viperid species (out of the 365 known so far), making this the most comprehensive work on the evolution of caudal luring, conspicuous tail tips, and ontogenetic shifts in diet from ectothermic to endothermic prey.

We found correlations among all three of these characters, as previously suggested in the literature (e.g. Neill 1960; Martins et al. 2002; Del Marmol et al. 2016). However, we also found that their occurrence is more strongly correlated with shared evolutionary history within Viperidae than with what might be expected due to ecological constraints. Additionally, we corroborated the hypothesis that these three characters may have been present in the Viperidae ancestor, with a high probability for this scenario, despite parsimony reconstruction suggesting independent emergences for ontogenetic shifts in diet.

Our results suggest that conspicuous tail morphology, specifically the presence of a different-colored tail tip, is closely associated with dietary shifts in vipers, indicating the tail-luring behavior as an adaptive hunting strategy. Although gaps in natural history data limit some aspects of our conclusions, this study highlights the importance of basic ecological research for understanding the evolution of these species, suggesting that further research should provide more information on the natural history of viperid snakes. Additionally, citizen science resources, especially when accompanied by verifiable information, can offer valuable information to fill those knowledge gaps. Future work should focus on integrating behavioral observations with morphological and dietary data to unravel the ecological and evolutionary drivers of tail-luring in vipers.

ACKNOWLEDGMENTS

We would like to thank the Programa de Pós-Graduação em Zoologia from the University of Brasilia for its academic and institutional support throughout the development of this research.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

This work was supported by the Coordination for the Improvement of Higher Education Personnel (CAPES) under Grant No. 88882.383281/2019-01; Conselho Nacional de Desenvolvimento Científico e Tecnólogico (CNPq) for a productivity grant [processes #306644/2020-7 and #401334/2025-2].

AUTHOR CONTRIBUTIONS

A.P. Giozza, V.Slobodian and R.A. Brandão conceived the ideas and designed the methodology; A.P. Giozza collected the data; A.P. Giozza, V. Slobodian and L.M. Diele-Viegas analysed the data; A.P. Giozza, R.S. Magalhães and M.O. Heliópolis led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTAL DATA

Supplemental Data for this article can be accessed online at https://doi.org/10.1080/03949370.2026.2630806

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Endnote

1. Note added in proof: since the analyses, more species were described or reallocated in Viperidae (see Uetz et al. 2026). Nevertheless, this does not change substantially the results found herein, but emphasize the urgency in collect more natural history data on Viperidae species.