

Convergent Evolution and Multifunctional Hypothesis of Supraocular Appendages in Viperidae

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Abstract. Supraocular appendages in Viperidae are iconic morphological traits with a long history of functional speculation, yet existing relevant literature remains fragmented and fails to establish an integrated functional framework. This paper systematically compiles morphological, ecological, developmental and behavioural data of viper supraocular appendages to conduct a critical reassessment of two classical hypotheses: crypsis and sexual ornamentation. Four representative species are selected as focal species: *Bothriechis schlegelii*, *Protobothrops cornutus*, *Pseudocerastes fieldi* and *Bitis cornuta*. These structures are redefined as multifunctional Supraocular Environmental Interfaces (SEIs) shaped by habitat-specific selective pressures through convergent evolution. Phylogenetic analyses identify at least four independent evolutionary origins of such appendages within Viperidae, and their distribution exhibits strong positive correlations with heavy precipitation, dense vegetation and aeolian exposure. A three-dimensional "drainage–buffer–probe" hypothesis is proposed for viper species dwelling in humid habitats, while a "sand-deflection–light-shading–mechanical-stabilisation" hypothesis is put forward for arid-dwelling taxa. The absence of homologous structures in Elapidae stems from conserved cephalic-shield developmental pathways and divergent foraging strategies, with the genus *Acanthophis* serving as a partial convergent exception. This paper summarises core unresolved research gaps and proposes targeted experimental directions to advance investigations into this complex adaptive trait, supplementing theoretical support for reptilian ecomorphology research.

Keywords: Supraocular appendage, convergent evolution, head shield fragmentation, environmental interface

1. Introduction

Among the most conspicuous morphological features of Viperidae are supraocular appendages, which can be observed in genera including *Bothriechis*, *Protobothrops*, *Pseudocerastes*, *Bitis* and *Cerastes* [1]. Since their first morphological documentation in the 19th century, academic interpretations of their biological functions have been confined exclusively to two perspectives: crypsis and sexual ornamentation [2]. Such conclusions are merely derived from static specimen observations and rough ecological correlations; systematic *in vivo* behavioural tracking and experimental evidence regarding sensory innervation are still absent [3]. In other words, a prominent

verification gap exists: this well-documented morphological trait has long lacked rigorous functional verification [3]. Most existing studies concerning viper cranial morphology and convergent evolution centre on venom systems or overall body plan adaptation, while few comprehensive cross-taxonomic syntheses focus specifically on supraocular appendage functions [4]. Isolated research records the morphology or behavioural traits of individual species, yet comparative analyses integrating developmental plasticity, habitat ecology and phylogeny remain scarce [5]. Additionally, traditional functional hypotheses have not been re-examined with updated morphological, behavioural and developmental datasets, leaving room for a unified, hypothesis-driven study [4]. The central argument of this research holds that supraocular appendages should not be reduced to visual signals or camouflage devices alone; instead, they can be defined as Supraocular Environmental Interfaces (SEIs) — multi-functional morphological structures formed by specialised periocular scales under specific ecological conditions [5]. The functional orientation of such interfaces varies by habitat type, rather than being fixed by phylogenetic relationships [6]. This paper organises all available evidence on the morphology and distribution of viper supraocular appendages, objectively evaluates the strengths and weaknesses of the crypsis and sexual ornamentation hypotheses, and constructs an integrated multifunctional SEI hypothesis via cross-species comparative analysis. It further interprets taxonomic differences in the presence or absence of supraocular appendages from developmental and ecological dimensions, and identifies key research gaps to guide subsequent empirical studies [7]. Four phylogenetically distant and ecologically differentiated species are selected for comparative analysis, and the developmental and ecological mechanisms behind the total absence of homologous structures in Elapidae are elaborated in detail [8].

2. Phylogenetic and developmental foundations of convergent evolution

2.1. Evidence for multiple independent origins

Bothriechis schlegelii belongs to the subfamily Crotalinae and the genus *Bothriechis*, inhabiting the upper canopy of Central American tropical rainforests [1]. *Protobothrops cornutus* is also classified under Crotalinae but falls within the genus *Protobothrops*, distributed in the understory of subtropical evergreen-deciduous mixed forests in southern China. Despite their distant phylogenetic relationship within Crotalinae, the two species evolve highly analogous supraocular structural systems: both derive from keratinous hyperplasia of the supraocular scale, contain no bony core, and fail to form direct articulation with the skull [9]. *Pseudocerastes fieldi* belongs to Viperinae, genus *Pseudocerastes*, is distributed across arid deserts and shrublands of the Middle East. *Bitis cornuta* is another viperine species of the genus *Bitis*, inhabiting rocky coastal deserts of South Africa and Namibia. Though they belong to distinct viperine clades, both independently evolve horn-like supraocular protrusions [6]. Phylogenetic comparative analyses confirm a minimum of four independent origins of this structure within Viperidae [4]. The distribution pattern of supraocular appendages does not align with phylogenetic topology, yet it shows significant positive correlation with precipitation intensity, vegetation coverage and aeolian erosion [6]. This represents a classic example of adaptive convergent evolution, rather than retention of ancestral traits [10].

2.2. Structural prerequisites of developmental plasticity

Viperidae possess solenoglyphous venom apparatuses that induce lateral skull compression and cephalic-shield fragmentation, which enables developmental plasticity within the periocular region

[9]. A broad developmental boundary exists between supraocular and frontal scales, where mutations triggering keratinous hyperplasia can be phenotypically expressed [9]. Cephalic-shield fragmentation is especially prominent in Viperinae; excluding the genus *Causus*, all other viperine taxa lose the nine integrated large dorsal head shields and develop smaller, irregularly arranged tiny scales [4]. In contrast, Elapidae maintain highly conserved cephalic-shield layouts, lacking the developmental window required for such scale mutation to emerge [8]. Accordingly, supraocular appendages can be regarded as a unique evolutionary product exclusive to Viperidae, rather than a plesiomorphic trait shared by all snakes [10].

3. Traditional functional hypotheses: crypsis and sexual ornamentation

3.1. Crypsis hypothesis

The crypsis hypothesis claims that supraocular appendages break the snake's head contour to achieve camouflage [2]. Correlative evidence links prominent horn structures to complex microhabitats, yet this theory cannot explain three core phenomena: the exclusive distribution of such traits within Viperidae, interspecific morphological divergence, and the absence of supraocular horns in open-habitat viper species [1].

3.2. Sexual ornamentation hypothesis

The sexual ornamentation hypothesis posits that supraocular protrusions serve as indicators of individual mate quality [3]. This view lacks sufficient supporting evidence due to weak sexual dimorphism across horned viper species and a complete absence of recorded courtship or agonistic behaviours mediated by horn morphology [3]. Juvenile individuals also develop fully formed supraocular appendages, proving these structures do not solely function for sexual selection [5]. Taken together, the two classical hypotheses only provide fragmented explanatory power and have not been validated through controlled experiments. A habitat-dependent multifunctional framework can reconcile all contradictory observational phenomena recorded in existing literature [4].

4. Humid-habitat SEI: the drainage–buffer–probe hypothesis

4.1. *Bothriechis schlegelii*

Bothriechis schlegelii inhabits tropical rainforest canopies with annual precipitation often exceeding 3000 mm, where vertical rainfall and canopy drips constitute the primary hydrological disturbance [1]. Its supraocular appendages are soft, multi-branched and eyelash-shaped with passive flexibility [9]. From a biomechanical perspective, the branch-like flow-guiding structures laterally deflect vertical raindrops away from the visual axis, reducing corneal water accumulation and optical scattering [5]. Rainforest ambush predators generally exhibit poor visual acuity; even a thin water film covering the cornea drastically degrades imaging contrast [5]. Therefore, the drainage function constitutes the primary adaptive advantage of SEIs for viper species in high-precipitation zones [5].

4.2. *Protobothrops cornutus*

Protobothrops cornutus resides in subtropical deciduous forest understories covered by thick litter layers prone to seasonal heavy rainfall and frequent falling branches. Its supraocular horns are short and blunt, also formed by keratinous hyperplasia of specialised supraocular scales [9]. Unlike the

delicate branched structures of *B. schlegelii*, the thick, flexible horns of *P. cornutus* create a buffer zone to prevent direct corneal contact with fallen leaves and twigs [5]. Field observations show that individuals often half-bury their heads in litter substrates during rest. The horn tip bears the brunt of mechanical impact and dissipates force via elastic deformation, acting as a passive shock absorber [5].

4.3. Shared function: wedge-shaped visual windows and spatial manipulation

For both humid-habitat species, horn tips can be wedged into leaf axils or propped against overlapping foliage to form wedge-shaped observation windows for stationary ambush predation [5]. This function reduces the exposure risk associated with large-scale head movements to adjust vision. Conventionally, snakes must lift or rotate their heads to expand the visual field; SEIs enable effective environmental monitoring with minimal cranial displacement [4]. Captive breeding records show that *Bothriechis schlegelii* frequently inserts horn tips into petiole joints to fix its observation posture while coiling on branches, whereas *Protophops cornutus* utilises horn protrusions to push aside litter obstructions and maintain vigilance over surrounding movement trails [5].

5. Arid-habitat SEI: the sand-deflection–light-shading–mechanical-stabilisation hypothesis

5.1. *Pseudocerastes fieldi*

Pseudocerastes fieldi is distributed across arid zones of the Middle East, including the Sinai Peninsula, Israel, Jordan, northwestern Iraq and northern Saudi Arabia. It inhabits basalt platforms, limestone outcrops and muddy flats, avoiding mobile shifting sand dunes [6]. Its supraocular horn consists of clustered small scales forming a rigid triangular cone protruding above the eye, far stiffer than the soft appendages of rainforest viper species [6]. Wind-blown sand represents the dominant selective pressure in desert habitats [6]. Near-ground crosswinds carry high-speed sand particles that scratch and abrade the cornea upon direct contact [6]. The horn-shaped structure acts as a passive aerodynamic deflector, diverting sand-laden air currents away from ocular tissue and lowering corneal abrasion frequency [5]. This species is predominantly nocturnal and shelters within rock crevices or shrub root systems during daylight hours [6]. At rest, only the horn protrudes above the substrate; together with rough dorsal scales, it disrupts head contour and achieves rock-mimicking camouflage [2].

5.2. *Bitis cornuta*

Bitis cornuta occupies rocky deserts, dwarf succulent shrublands and mountain fynbos along the Atlantic coast of South Africa and Namibia, regions characterised by persistent wind, high evaporation and extreme diurnal temperature fluctuation. Each eye bears 2–5 clusters of horn scales, creating a multi-horned morphology [6]. Compared with the single conical horn of *P. fieldi*, its clustered horn structure presents a wider three-dimensional outline [5]. Captive behavioural observations classify *Bitis cornuta* as a specialised burrowing viper, which gradually sinks its head into loose sand via lateral body undulations, leaving only eyes and horn tips exposed on the surface [5]. The clustered horn array delivers two core adaptive benefits: First, moderate light-shading capability. During short morning and evening surface activities, horn tips cast uneven shadows on the cornea to attenuate intense solar radiation, avoiding retinal damage and glare interference [5]. Second, mechanical anchoring. Dense horn clusters expand contact area between the head and

substrate, stabilising ambush posture against wind and sand flow displacement [6]. Collectively, these structures protect ocular tissue from sand abrasion and assist camouflage by disrupting head silhouette [2].

5.3. Morphological–functional divergence between arid and humid SEI types

The four focal species develop morphologically distinct SEIs corresponding to their respective ecomorphotypes [4]. Soft, pliable branched horns of humid viper species prioritise drainage and shock-buffering performance; rigid conical or clustered horns of desert taxa specialise in sand deflection and substrate anchoring [6]. The morphology-function mapping relationship fully supports the multifunctional SEI hypothesis: horn shape is primarily driven by local habitat stressors rather than phylogenetic constraints [10].

6. The systematic absence in elapidae and the exception of acanthophis

6.1. The conserved cephalic-shield pattern

Over 3,000 recorded elapid and colubrid species lack periocular structures with developmental and structural homology to viperid SEIs [8]. Elapidae retain an extremely conservative head-shield layout: along the dorsal midline lie the rostral scale, paired internasals, paired prefrontals, a single frontal scale and paired parietals, forming eight integrated large dorsal head shields [8]. A single preocular scale, 2–3 postocular scales and continuous upper labial scales encircle the eye region. The supraocular scale forms an intact large shield with fixed sutural boundaries on the front and lateral sides [9].

6.2. Foraging ecology and the absence of selective pressure

Most Elapidae are active pursuit predators or generalist opportunists, adopting continuous chasing and rapid striking instead of prolonged sit-and-wait ambush [8]. Even semi-fossorial and terrestrial elapid taxa burrow through leaf litter and soil with constant cranial friction against substrates [11]. Any protruding horn-like structure would increase locomotion resistance and suffer frequent abrasion [3]. Additionally, few elapid species exhibit substrate-embedded ambush requiring partial head submersion in sand or litter, removing the selective pressure driving sand deflection, rainfall drainage and mechanical buffering functions [8]. Niche differentiation explains the total absence of SEIs within Elapidae. The full functional spectrum of supraocular appendages (rain drainage, sand shielding, mechanical buffer) tightly correlates with ambush-burrowing ecology, an adaptive niche that Elapidae have never evolved to occupy [10].

6.3. The exception of acanthophis

Genus *Acanthophis* is distributed across Australia and New Guinea, the only elapid lineage evolving supraocular horn-like protrusions [12]. All species within this genus carry paired raised bumps derived from modified supraocular scales [8]. Nevertheless, their structures differ fundamentally from viperid SEIs in developmental origin and tissue composition: death adder horns merely represent local thickening of a single supraocular shield, rather than composite multi-scale branched structures [9]. These rigid protrusions lack the soft flexible texture of rainforest viper appendages [12]. The cephalic horns of *Acanthophis* constitute a typical case of partial convergent evolution [10]. As highly specialised ambush elapids, they occupy an ecological niche analogous to terrestrial

vipers, independently evolving flattened triangular heads, compact robust bodies and caudal luring behaviour [12]. Ecological convergence unlocks limited developmental potential of supraocular scales [8]. Restricted by Elapidae's rigid conserved cephalic-shield developmental programme, however, Acanthophis cannot develop the morphological complexity and multifunctionality of viperid SEIs [8]. The existence of death adders proves the evolution of supraocular appendages requires dual preconditions: ambush-burrowing ecological pressure and developmental plasticity via cephalic-shield fragmentation. Elapidae only partially satisfy the ecological prerequisite through Acanthophis, yet remain constrained by inflexible head-scale developmental pathways [10].

7. From ornament to environmental interface

7.1. Critical re-examination of traditional hypotheses

The classical crypsis theory cannot account for the exclusive distribution of supraocular appendages within Viperidae (plus the single elapid exception Acanthophis), despite widespread camouflage reliance among Elapidae and Colubridae [2]. If horns function solely as visual disguise, this trait would spread far more broadly across snake phylogeny [1]. The sexual ornamentation hypothesis also lacks solid empirical support: both male and female horned vipers develop fully mature appendages under captive breeding, and no documented mate choice or intrasexual competition behaviours rely on horn size [3]. In contrast, the SEI hypothesis links structural morphology to measurable physical habitat conditions, logically explaining cross-lineage convergent origins, interspecific ecomorphological differentiation and the universal absence of homologous structures within Elapidae [4].

7.2. Unresolved questions of innervation and sensory potential

Systematic neuroanatomical tracing of SEI innervation has not yet been conducted [3]. If mechanoreceptors or thermoreceptors concentrate at horn tips, SEIs would operate as active sensory detectors rather than passive physical buffers [5]. For instance, the branched eyelash horns of *Bothriechis schlegelii* may sense raindrop impact frequency and direction to trigger rain-avoidance behaviours; horn tips of *Bitis cornuta* could detect sand vibration to adjust burrowing depth accordingly [5]. Future research may utilise immunohistochemistry and neural tracing techniques to map sensory nerve distribution within supraocular appendages [9].

7.3. Methodological value of captive observations

Multiple core inferences in this study originate from long-term captive behavioural monitoring [5]. Although captive environments cannot fully replicate wild habitats, controlled lab trials eliminate confounding variables to isolate single functional traits for targeted testing [11]. For illustrative experimental design: under simulated heavy rainfall sprays, *Bothriechis schlegelii* individuals with surgically removed horns accumulate far more corneal surface moisture than intact controls; within wind-sand simulation chambers, hornless *Bitis cornuta* display significantly higher spectacle abrasion rates and ocular irritation signs [5]. Such testable predictions provide clear directions for subsequent field verification research [7].

8. Conclusion

The supraocular appendages of *B. schlegelii*, *P. cornutus*, *P. fieldi* and *B. cornuta* emerge from convergent evolution driven by distinct habitat selective pressures including rainwater drainage, mechanical shock absorption, sand deflection and light attenuation, rather than simple crypsis or sexual selection. These structures should be redefined as Supraocular Environmental Interfaces (SEIs), whose specific adaptive functions shift based on dominant local ecological stressors. Humid-habitat viper SEIs evolve soft branched drainage–buffer–probe structures, while arid-species SEIs form rigid conical sand-deflection–light-shading–mechanical-stabilisation morphologies. The total absence of equivalent periocular structures within Elapidae arises from dual developmental and ecological constraints: highly conserved cephalic-shield patterning and an active pursuit foraging strategy. The genus *Acanthophis* represents the sole partial exception, developing simplified horn-like protrusions after evolving ambush predation. Three research pathways are proposed to fill current experimental verification gaps: first, cross-species in vivo behavioural quantification to measure SEI functional contributions under rainfall, wind-sand and mechanical impact treatments; second, high-resolution CT scanning and histological sectioning to compare keratin microstructure, vascular distribution and innervation patterns across the four focal species; third, developmental molecular biology to identify gene regulatory pathways governing supraocular scale keratin hyperplasia, uncovering the genetic basis of this convergent morphological trait. Integrated morphological description, functional experimentation and evolutionary developmental analysis are required to fully elucidate the adaptive advantages of this iconic viperid trait. This research also offers preliminary bioinspiration for fluid-resistant biomimetic structural design.

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