Trabajo

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The eye in nocturnal dipsadines *Atractus crassicaudatus* and *Sibon nebulatus* (Serpentes: Dipsadinae): variations associated with lifestyle

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ABSTRACT

Snakes possess a complete eye and share similarities with other reptiles, although they present features such as the spectacle that replaces the movable eyelid. They also exhibit interspecific variations in eye size, and spectacle and corneal thickness associated with lifestyle and diel activity. We compared ocular morphology in two nocturnal dipsadine species, the fossorial *Atractus crassicaudatus* and the arboreal *Sibon nebulatus*, using histological analyses to examine for lifestyle-associated differences. *A. crassicaudatus* has smaller eyes than *S. nebulatus,* as well as a thinner spectacle and cornea, a very small to absent anterior chamber, a subspherical lens, and thin retinal nuclear layers. *S. nebulatus* has a larger eye, thicker spectacle and cornea, a distinct anterior chamber, a spherical lens, and thick retinal nuclear layers. The suite of characters in *A. crassicaudatus* is consistent with reduced reliance on vision in a fossorial context, whereas *S. nebulatus* exhibits traits compatible with enhanced visual capacity in an arboreal setting. We conclude that dipsadine snakes exhibit morphological variations in the eye, possibly associated with lifestyle, as observed here between a fossorial and an arboreal species.

Key words: Eyeball; Habitat; Natural History; Morphology; Serpentes.

RESUMEN

Las serpientes poseen un ojo completo y comparten similitudes con otros reptiles, aunque presentan rasgos como la escama ocular que reemplaza al párpado móvil. También exhiben variaciones interespecíficas en el tamaño del ojo, y en el grosor de la escama ocular y la córnea, asociadas con el modo de vida y la actividad. Comparamos la morfología ocular en dos especies nocturnas de dipsadinos, la fosorial *Atractus crassicaudatus* y la arborícola *Sibon nebulatus*, mediante análisis histológicos para examinar diferencias asociadas con el modo de vida. *A. crassicaudatus* tiene ojos más pequeños que *S. nebulatus*, así como una escama ocular y una córnea más delgadas, una cámara anterior muy pequeña o ausente, una lente subesférica, y capas nucleares retinianas delgadas. *S. nebulatus* tiene un ojo más grande, una escama ocular y una córnea más gruesas, una cámara anterior distintiva, una lente esférica, y capas nucleares retinianas gruesas. El conjunto de caracteres en *A. crassicaudatus* es consistente con una menor dependencia de la visión en un contexto fosorial, mientras que *S. nebulatus* exhibe rasgos compatibles con una capacidad visual mejorada en un entorno arborícola. Concluimos que las serpientes dipsadinas exhiben variaciones morfológicas en el ojo, posiblemente asociadas con el modo de vida, como se observó aquí entre una especie fosorial y una arborícola.

Palabras claves: Globo ocular; Hábitat; Historia natural; Morfología; Serpentes.

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Introduction

The reptilian eye shares the general bauplan of vertebrates and shows relatively modest intergroup variation (Walls, 1942; Wyneken, 2012). Typically, reptiles possess movable eyelids, a cornea, anterior chamber, pupil, iris, posterior chamber (together with the anterior chamber filled with aqueous humor), lens, vitreous chamber (with vitreous humor), and retina (Walls, 1942; Underwood, 1970).

Snake eyes differ in two major ways. First, they are externally covered by an immobile, transparent spectacle formed embryologically by fusion of the eyelids (Walls, 1942; Bellairs & Underwood, 1951; Underwood, 1970; Sivak, 1977; Da Silva *et al.*, 2014, 2015a, 2015b, 2017). This structure is thought to have evolved to provide protection against external abrasion, consistent with a fossorial origin of snakes (Walls, 1940, 1942; Da Silva *et al.*, 2014, 2017). Second, accommodation is achieved primarily by iris-driven pressure on the vitreous humor that translates the lens anteroposteriorly (Sivak, 1977), rather than by ciliary muscle deformation of the lens as in most other reptiles (Underwood, 1970; Caprette *et al.*, 2004). Notably, snakes also lack the scleral ossicles/cartilage present in several other lepidosaurs; because this scleral skeleton normally provides the rigid support needed for ciliary-driven lens deformation, its absence is thought to be mechanically linked to the reliance on lens translation rather than lens-shape change for accommodation (Walls, 1942; Underwood, 1970).

Ocular morphology varies with natural history, including lifestyle and diel activity (Brischoux *et al.*, 2010; Foureaux *et al.*, 2010; Liu *et al.*, 2012; Da Silva *et al.*, 2017, 2019; Huang *et al.*, 2022). Across 14 families (including Colubridae), nocturnal species tend to have smaller eyes than diurnal species; fossorial taxa have smaller eyes than taxa with other lifestyles; and terrestrial and arboreal species have thinner spectacles than aquatic and fossorial taxa (Da Silva *et al.*, 2017, 2019).

Internal ocular structures also vary. *Typhlops*, a fossorial genus, has reduced eyes with a thick spectacle, a rudimentary cornea, and a fused iris–ciliary body complex and lacks an anterior chamber (Foureaux *et al.*, 2010). Retinal organization also varies with ecology: fossorial and nocturnal lineages (Aniliidae, Leptotyphlopidae, Typhlopidae, Uropeltidae) often have rod-only retinas, whereas some diurnal colubrids have cone-only retinas; arboreal Boidae and Colubridae can have duplex retinas with rods and cones (Walls, 1940; Underwood, 1970; Caprette, 2005; Hauzman *et al.*, 2014, 2017; Hauzman, 2020).

The Dipsadinae, the most diverse snake subfamily within Colubridae, provide a useful model for exploring such axes of variation, as they are widely distributed in the Americas, found in different ecosystems, and vary in lifestyle and activity patterns (Pandelis *et al.*, 2023; Uetz *et al.*, 2025). Here, we compare ocular anatomy in two nocturnal dipsadines that differ markedly in their natural history. *Atractus crassicaudatus* is a fossorial predator that actively forages for earthworms and other soft-bodied invertebrates low in root thickets, under rocks, and in other fossorial environments, whereas *Sibon nebulatus* is an arboreal snail specialist that searches for gastropods in vegetation (Paternina-Cruz & Capera, 2017; Pazmiño-Otamendi, 2020). We assessed whether the contrasting lifestyles of these species are associated with differences in eye structure. Insights from such comparisons can illuminate the evolution of snake visual systems.

Materials and methods

We examined six eyes in total: three from *A. crassicaudatus* and three from *S. nebulatus*, derived from two individuals per species. Both *A. crassicaudatus* specimens and one *S. nebulatus* specimen are housed in the Laboratorio de Biología Animal, Departamento de Biología, Universidad Nacional de Colombia, Sede Bogotá; these specimens were donated by collectors who found them dead. The second *S. nebulatus* specimen is ICN-R-14219, a preserved museum specimen from the Reptile Collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Sede Bogotá. All specimens were previously fixed in formalin and preserved in 70% ethanol.

Eye removal followed species-specific procedures. Initial attempts to excise the eye directly in *A. crassicaudatus* consistently resulted in detachment of the spectacle; therefore, a ~5 × 5 mm block encompassing the eye, skin, muscles, and bones was extracted to preserve this structure. In *S. nebulatus*, direct eye excision was possible by tracing the orbital contour with a dissecting needle to incise the integument. Next, a fine-tipped forceps was introduced at the middle-posterior region of the orbit, advanced to the innermost part of the skull, and gentle force was applied to excise the eye.

Each eye was fixed in 10% formaldehyde for 24 h, and then post-fixed in 4% formaldehyde + 2% glutaraldehyde for 24 h (Caprette, 2005). Samples were sent to the Laboratorio de Patología Veterinaria, Facultad de Medicina Veterinaria, Universidad Nacional de Colombia, Sede Bogotá for hematoxylin–eosin histology.

The heads and eyes of the snakes were photographed on graph paper with a Zeiss Stemi 305 stereomicroscope, diameters were measured in ImageJ (v1.54, x64), and snout–vent length (SVL) was measured using a flexible measuring tape. Eye size was defined as the total globe diameter after removal. All other measurements were made perpendicular to the spectacle surface and were reported as means of five readings per structure, which were obtained from images captured on a Nexcope NE-300 microscope using ImageView (v4.11.23945, x64). Axial and equatorial lens diameters were measured along two axes defined relative to the globe, with the axial direction running from the spectacle to the optic nerve through the center of the eye, and the equatorial direction perpendicular to the axial direction in the dorsoventral plane.

Histological terminology follows Caprette (2005), Underwood (1970), Walls (1940, 1942), and Wyneken (2012). Figures depict the highest-quality sections from one individual per species (left eye for *A. crassicaudatus*; right eye for *S. nebulatus,* specimen ICN-R-14219). We first describe *A. crassicaudatus* and then highlight differences in *S. nebulatus*.

Results

Histological features of the eye in *Atractus crassicaudatus*

Atractus crassicaudatus has a subspherical eye measuring 1.73 ± 0.21 mm in diameter (Fig. 1A). Key structures are summarized below to emphasize species-specific features.

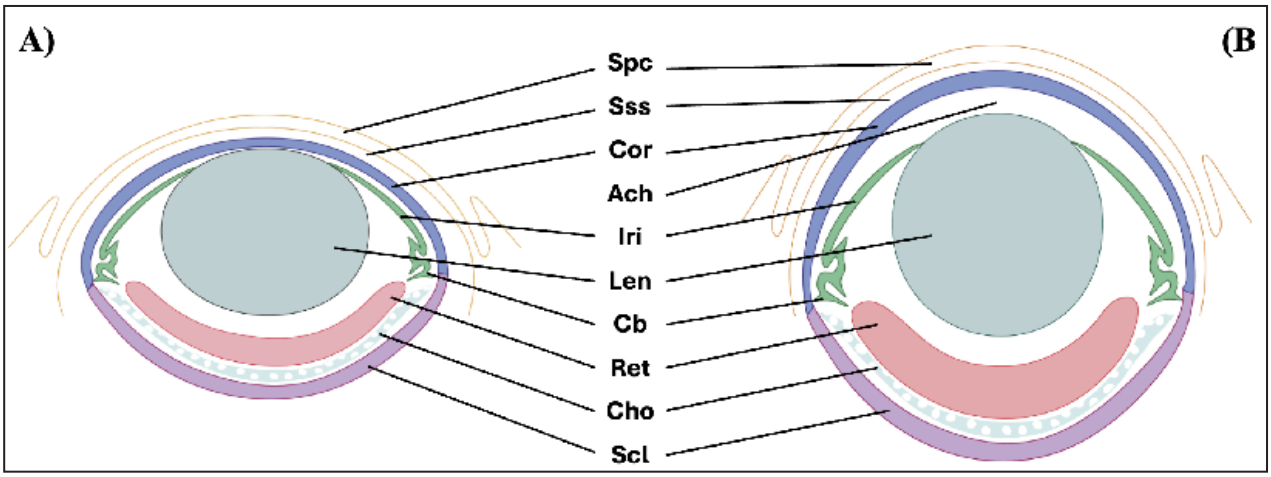

Figure 1. Structural diagram of the eye of *Atractus crassicaudatus* (A) and *Sibon nebulatus* (B). Abbreviations: Ach – anterior chamber; Cb – ciliary body; Cho – choroid; Cor – cornea; Iri – iris; Len – lens; Ret – retina; Scl – sclera; Spc – spectacle; Sss – sub-spectacular space.

The spectacle

The spectacle in *A. crassicaudatus* is shallowly curved, 33.0 ± 0.38 µm thick, and comprises three layers: outer epithelium (Oe), stroma (Str), and inner epithelium (Ine; Fig. 2A). The outer epithelium includes a germinal layer of squamous cells with granular, basophilic oval nuclei; a second squamous layer with less conspicuous nuclei; and an external, thick acellular keratin layer (Q), which was detached in two large blocks during sectioning. The stroma consists of 4–7 uniform, thin collagen lamellae with interspersed fibroblasts (Fib) bearing elongated basophilic nuclei and occasional blood vessels. The inner epithelium is a simple squamous layer with inconspicuous, elongated nuclei that borders the sub-spectacular space separating the spectacle from the cornea (Fig. 1A).

The cornea

In *A. crassicaudatus*, the cornea lies close to the lens; the anterior chamber between the cornea and lens is therefore absent (Figs. 1A, 2C). The cornea is 25.8 ± 1.12 µm thick and includes an outer corneal epithelium (Oec) and corneal stroma/substance

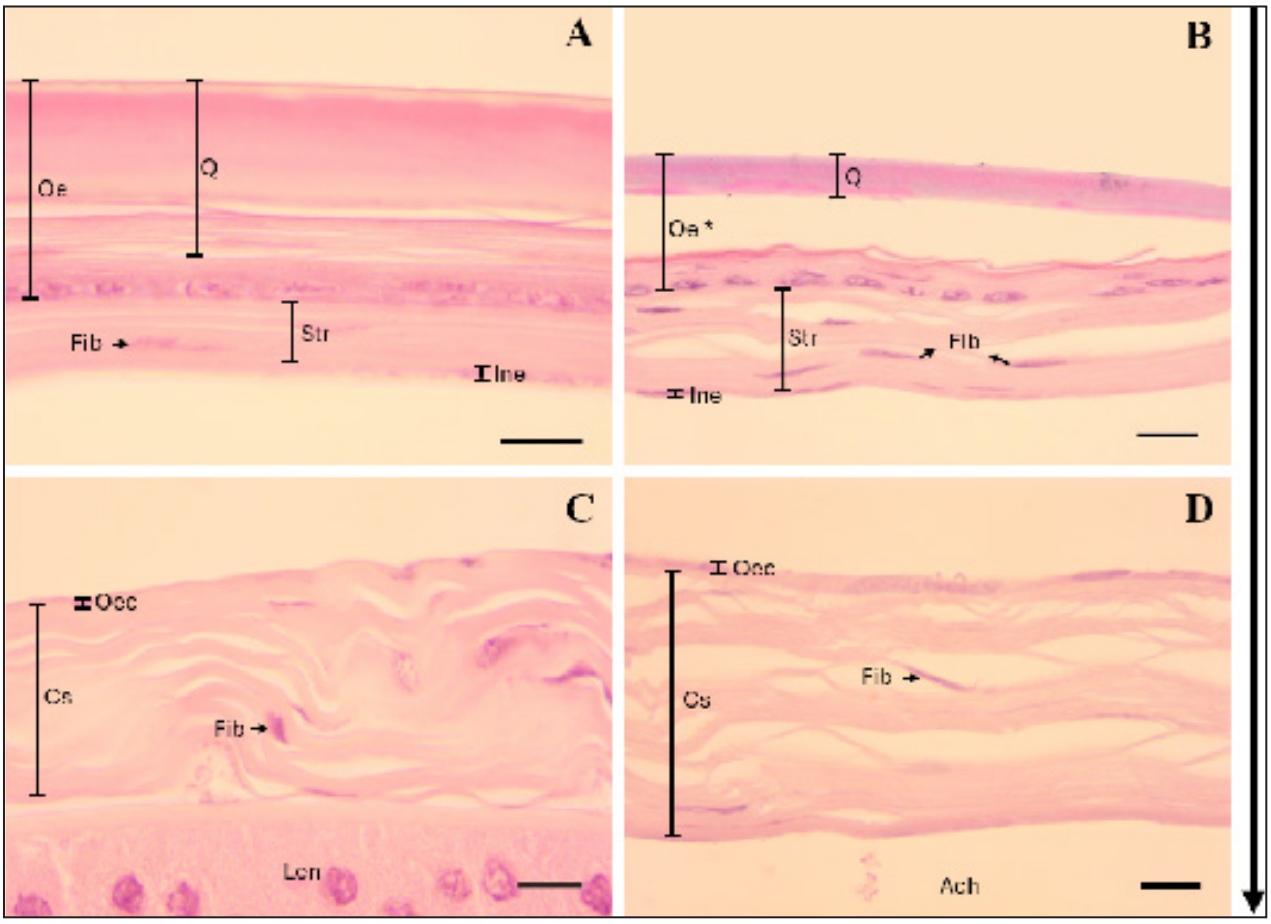

Figure 2. Cross-sections of the spectacle in *A. crassicaudatus* (A; scale bar = 10 μm) and *S. nebulatus* (B; scale bar = 25 μm), and of the cornea in *A. crassicaudatus* (C; scale bar = 7 μm) and *S. nebulatus* (D; scale bar = 10 μm). All sections stained with hematoxylin and eosin, 1000×. Abbreviations: Ach – anterior chamber; Cs – corneal substance; Fib – fibroblasts; Ine – inner epithelium; Len – lens; Oe – outer epithelium; Oec – outer corneal epithelium; Q – keratin layer; Str – stroma. The arrow indicates the direction of light entry. *In *S. nebulatus*, the keratin layer detached from the rest of the spectacle epithelium.

(Cs). The Oec is a simple squamous epithelium with fine, elongated nuclei. The corneal substance comprises 6–12 lamellae oriented parallel to the surface and showing gentle undulation; waviness increases toward the equator, forming an S-shaped pattern (Fig. 2C), with elongated fibroblast nuclei between lamellae.

Ciliary body, choroid, and sclera

The ciliary body (Cb) and iris (Iri) form a coupled iris–ciliary complex situated between the cornea (Cor) and lens (L; Figs. 1A, 3). The iris is heavily pigmented and vascularized. Peripherally, the sclera (Scl) constitutes the outer coat with 5–8 homogeneous lamellae bounded internally and externally by pigmented layers; it is thick near the ciliary body, thins equatorially, then thickens posteriorly. The choroid (Cho), between the retina (R) and sclera, is a thin, loose, vascular layer with external pigmentation, scattered fibroblasts, and rounded lacunae (Fig. 3).

The lens

The lens is subspherical (Figs. 1A, 4A) with an axial diameter of 752 ± 21.3 μm and an equatorial diameter of 882 ± 25.1 μm. It comprises the lens capsule (Lcap), subcapsular epithelium (Sube), and lens fiber layer (Lfib). The acellular, homogeneous capsule bounds the lens. Anteriorly, the subcapsular epithelium is tall, columnar, pseudostratified, with round basophilic nuclei situated mid-apically (Fig. 4C). Toward the equator, the epithelium grades from simple cuboidal to simple squamous and then disappears. Internally, the fiber layer consists of concentric, smooth lamellae forming a uniform structure. The apparent empty space within the lens

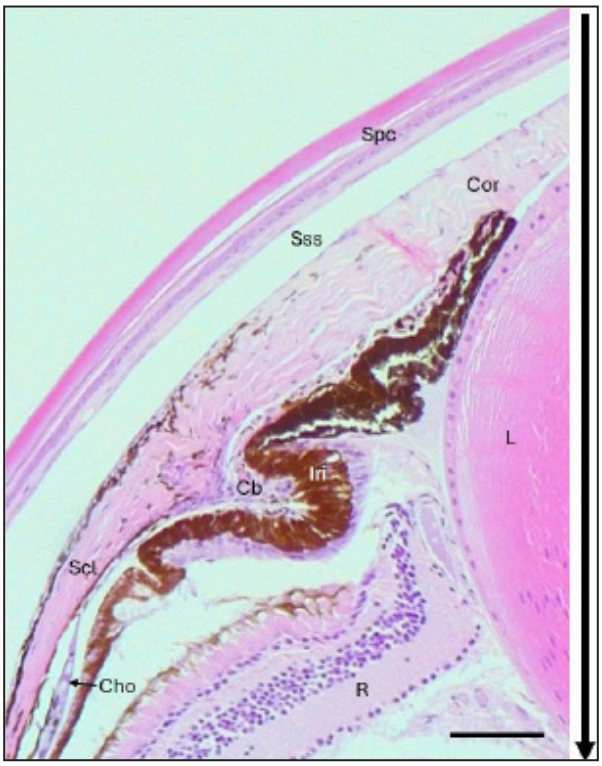

Figure 3. Cross-section of the eye of *Atractus crassicaudatus* (hematoxylin and eosin, 400×). Scale bar = 50 µm. Abbreviations: Cb – ciliary body; Cho – choroid; Cor – cornea; Iri – iris; L – lens; R – retina; Scl – sclera; Spc – spectacle; Sss – sub-spectacular space. The arrow indicates the direction of light entry.

(Fig. 4A) is a technical artifact produced during histological processing.

The retina

The retina of *A. crassicaudatus* is 91.2 ± 7.75 µm thick (Fig. 1A) and comprises, from the vitreal to the scleral side: ganglion cell layer (Gcl), inner plexiform layer (Plxi), inner nuclear layer (Inl), outer plexiform layer (Plxo), outer nuclear layer (Onl), and the photoreceptor layer (Phr; Fig. 5A). The Inl is 20.7 ± 2.77 µm (4–7 rows of nuclei), and the Onl is 5.25 ± 1.61 µm (1–2 rows).

The Phr contains small single cones (Ssc), large single cones (Lsc), and rods (Rod; Fig. 5C). Both cone types have oval inner segments wider than their outer segments, with a short myoid; Ssc have smaller inner and outer segments. Cone outer segments contact the pigmented layer, and no oil droplets were observed in the cone photoreceptors. Rods have a small, slightly globose inner segment and a long, thin outer segment.

Histological features of the eye in *Sibon nebulatus*

S. nebulatus has a spherical eye (Fig. 1B) measuring 4.47 ± 0.18 mm (Table 1). Differences relative to *A. crassicaudatus* are summarized below.

The spectacle is 82.4 ± 5.27 µm thick (Fig. 2B; Table 1); in all sections, the keratin layer detached from the outer epithelium (Fig. 2B). The cornea is 46.8 ± 1.45 µm thick, and lies farther from the lens owing to the presence of a distinct anterior chamber (Ach; Figs. 1, 2D). The corneal substance has 17–22 lamellae (Fig. 2D; Table 1). The sclera comprises 10–15 lamellae. Due to tissue quality, the ciliary body (Cb), iris (Iri), and choroid (Cho) were not clearly resolved. The lens (L) is large and spherical, with axial and equatorial diameters of 1905 ± 45.3 µm and 1918 ± 54.9 µm, respectively (Figs. 1B, 4B; Table 1). The retina (R) is thick (238 ± 25.7 µm), with 6–8 rows of nuclei in both Inl and Onl (Fig. 5B; Table 1). Small and large single cones (Ssc, Lsc) have an extremely long myoid followed by a globose ellipsoid, and a thin outer segment (Ous). Structures compatible with double cones (Dc) were also observed, although their identity could not be unequivocally confirmed using light microscopy. Rods have short inner segments and long outer segments approaching, but not contacting, cone inner segments; thus, rod outer segments do not reach the pigmented layer (Pig; Fig. 5D).

Discussion

Overall, *A. crassicaudatus* and *S. nebulatus* share the canonical organization of the snake eye and showed no detectable intraspecific anatomical variation. Nonetheless, several structures differed in size and thickness (spectacle, cornea, lens, retina), consistent with lifestyle-linked divergence.

Eye diameter was markedly smaller in *A. crassicaudatus* than in *S. nebulatus*, both in absolute (1.73 ± 0.21 vs. 4.47 ± 0.18 mm; Table 1) and relative terms (0.143 vs. 0.281: Table 1), matching the broader pattern of smaller eyes in fossorial species and larger eyes in arboreal species (Liu *et al.*, 2012; Da Silva *et al.*, 2017). Larger eyes admit more photons (Martin, 1993), potentially aiding foraging and predator detection. Fossorial dipsadines likely rely more on chemosensory and tactile cues and face predominantly overhead predation risk (Weaver & Kardong, 2010), whereas arboreal species may benefit from vision to detect prey and threats approaching from multiple directions (Lillywhite & Henderson, 1993; Senter, 1999).

The characteristics of the spectacle of the

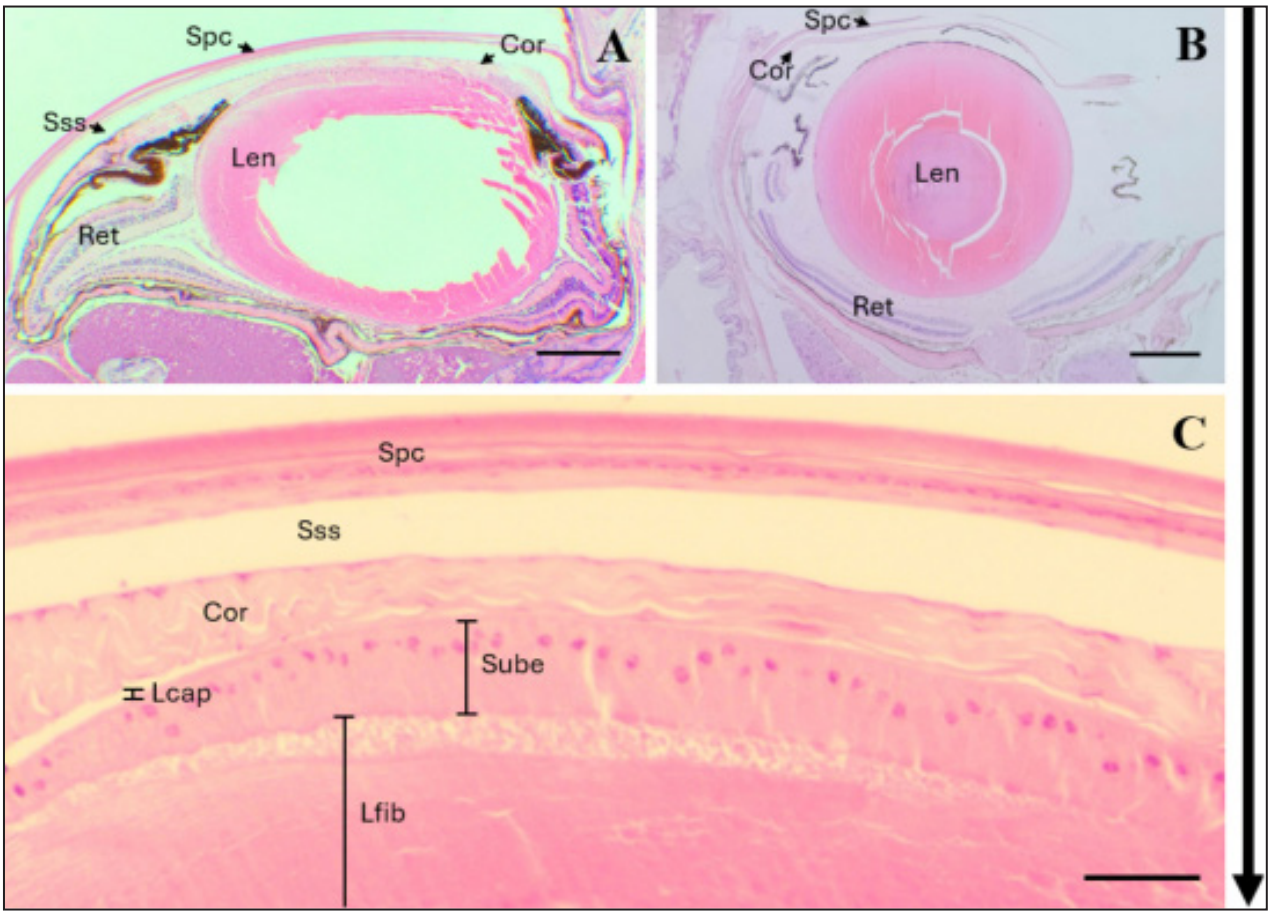

Figure 4. Eyes of (A) *Atractus crassicaudatus* (40×; scale bar = 200 μm) and (B) *Sibon nebulatus* (40×; scale bar = 500 μm), hematoxylin and eosin. (C) Close-up of *A. crassicaudatus* lens layers (100×; scale bar = 50 μm). Abbreviations: Cor – cornea; Len – lens; Lcap – lens capsule; Lfib – lens fibers; Ret – retina; Spc – spectacle; Sss – sub-spectacular space; Sube – subcapsular epithelium. The arrow indicates the direction of light entry.

dipsadines in our study were consistent with those observed in previous studies (Da Silva *et al.*, 2014, 2015a, 2015b). Absolute spectacle thickness was lower in *A. crassicaudatus* (33.0 μm) than in *S. nebulatus* (82.4 μm), but the relative value (thickness/eye size) was slightly higher in *A. crassicaudatus* (19.075 vs. 18.434). Da Silva *et al.* (2017) reported that fossorial species have a greater relative thickness of the spectacle compared with arboreal species, and even species with other lifestyles. Our findings are consistent with this pattern, indicating that fossorial snakes tend to possess relatively thicker spectacles than arboreal taxa, presumably reflecting higher protective demands (Walls, 1940; Da Silva *et al.*, 2017).

The characteristics of the cornea of the dipsadines in our study were also consistent with those observed in previous studies (Pchelyakov, 1981; Da Silva *et al.*, 2019). However, differences in thickness were found, as *S. nebulatus* presents a thicker cornea than *A. crassicaudatus* in absolute terms (46.8 ± 1.45 μm vs. 25.8 ± 1.12 μm). This pattern has been reported in snakes based on relative values, where arboreal species exhibit a thicker cornea compared to species with other lifestyles (Da Silva *et al.*, 2019). However, this was not observed in *A. crassicaudatus* and *S. nebulatus* (Table 1). Future studies are needed to explore how lifestyle influences corneal variation across a broader diversity of dipsadines, as well as clarify the functional role of the cornea.

The reptilian eye, like that of other vertebrates, typically possesses an anterior chamber between the cornea, iris, and lens, which contains aqueous humor (Wyneken, 2012). In the present study, a distinct anterior chamber was observed in *S. nebulatus*, whereas *A. crassicaudatus* lacked this space entirely. The absence of an anterior chamber in *A. crassicaudatus* has also been reported in other fossorial organisms, such as blind snakes (*Typhlops*) and amphisbaenians

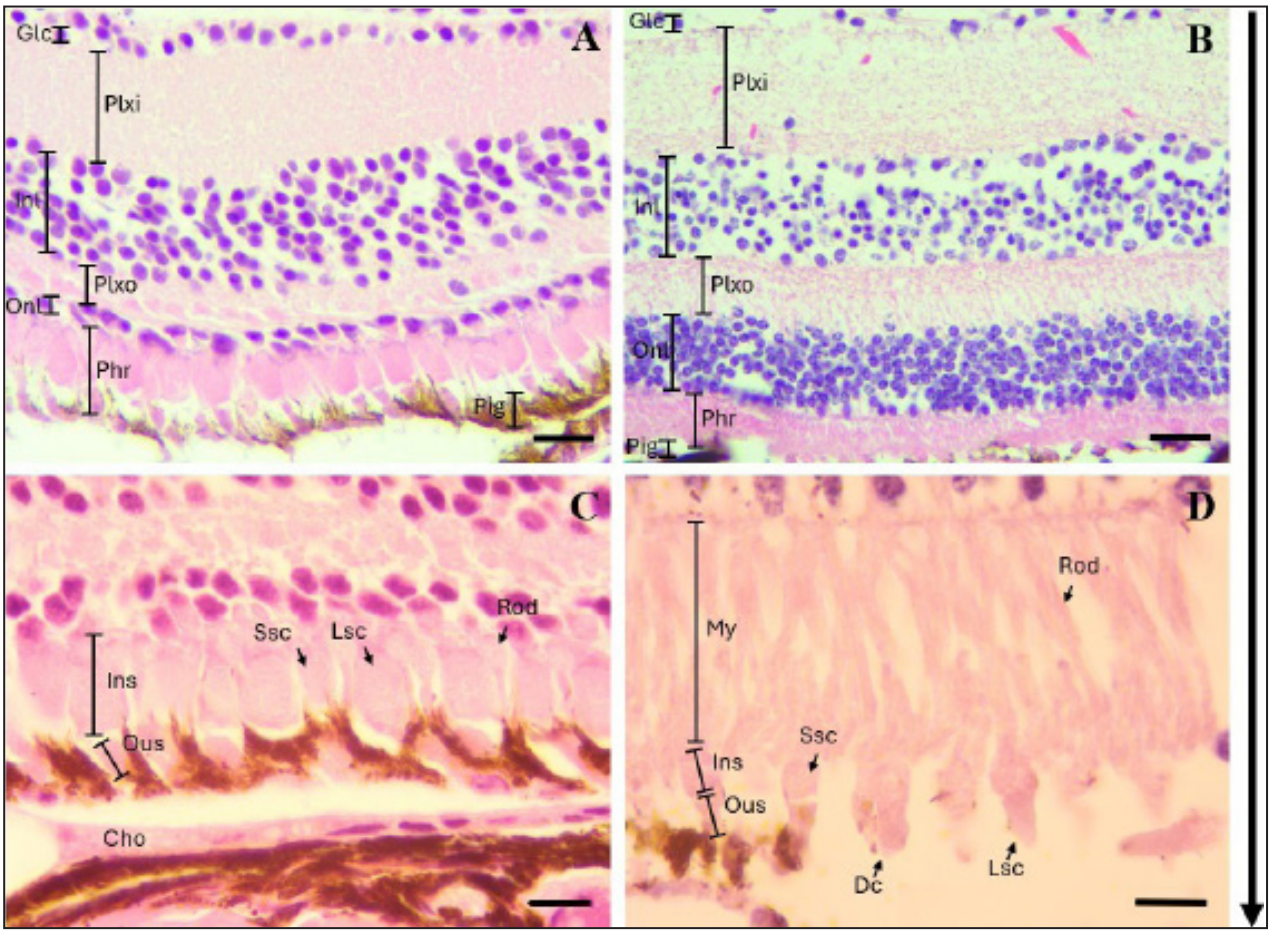

Figure 5. Retinas of (A) *Atractus crassicaudatus* (400×; scale bar = 15 µm) and (B) *Sibon nebulatus* (100×; scale bar = 30 µm), hematoxylin and eosin. Photoreceptors at higher magnification in (C) *A. crassicaudatus* and (D) *S. nebulatus* (1000×; scale bar = 10 µm). Abbreviations: Cho – choroid; Dc – double cone; Gcl – ganglion cell layer; Inl – inner nuclear layer; Ins – inner segment; Lim – limiting membrane; Lsc – large single cone; Onl – outer nuclear layer; Ous – outer segment; Phr – photoreceptor layer; Pig – pigmented layer; Plxi – inner plexiform layer; Plxo – outer plexiform layer; Rod – rod; Ssc – small single cone. The arrow indicates direction of light entry.

(Foureaux *et al.*, 2010). In contrast, the presence of an anterior chamber in *S. nebulatus* is consistent with visual evidence from cranial imagery published by Zaher *et al.* (2014), in which a clear separation between the cornea and lens can be observed, although ocular anatomy was not the focus of that study. The lack of aqueous humor associated with the absence of this chamber may reduce light refraction through the eye. Such a condition may reflect the reduced reliance on vision that characterizes many fossorial vertebrates, where subterranean environments impose low-light conditions and favor the reduction or simplification of visual structures (Walls, 1942). However, because our observations are based on preserved specimens and histological sections, the apparent absence of the anterior chamber should be interpreted with caution. Tissue fixation, dehydration, sectioning, and mounting can cause shrinkage or distortion of soft ocular tissues, potentially reducing the size of the anterior chamber. Although the anterior chamber was absent in all examined specimens of *A. crassicaudatus*, future studies using fresh material or in vivo imaging techniques will be necessary to determine whether this condition represents a true anatomical feature or is partially influenced by tissue processing.

Lens shape differed in *A. crassicaudatus* (subspherical) and *S. nebulatus* (spherical). Both lens shapes have been observed in various snake species, including in species in the family Colubridae (Walls, 1940; Sivak, 1977; Foureaux *et al.*, 2010). Spherical lenses may increase refractive power (Sivak, 1977) but can introduce spherical aberrations (Caprette, 2005; Mouy, 2024). Thus, *A. crassicaudatus* may experience less accommodative distortion despite lower lens power, whereas *S. nebulatus* may attain

Table 1. Main qualitative and quantitative differences in the eye between *Atractus crassicaudatus* and *Sibon nebulatus*. *Relative thickness of the structure, calculated as absolute thickness divided by eye size. **Relative eye size, calculated as total eye size divided by head size.

Difference	Structure	Measurement	A. crassicaudatus	S. nebulatus
Qualitative	Eye	Eye shape	Subspherical	Spherical
	Anterior chamber	Presence/absence	Absent	Present
	Lens	Lens shape	Subspherical	Spherical
Quantitative	Body	SVL (mm)	285 ± 24	536 ± 57
	Head	Head size (mm)	12.07 ± 0.87	15.92 ± 1.06
	Eye	Total eye size (mm)	1.73 ± 0.21	4.47 ± 0.18
		Relative eye size	0.143**	0.281**
	Spectacle	Total spectacle thickness (µm)	33.0 ± 0.38	82.4 ± 5.27
		Relative spectacle thickness	19.075*	18.434*
	Cornea	Total corneal thickness (µm)	25.8 ± 1.12	46.8 ± 1.45
		Relative corneal thickness	14.913*	10.470*
	Lens	Axial diameter (µm)	752 ± 21.3	1905 ± 45.3
		Equatorial diameter (µm)	882 ± 25.1	1918 ± 54.9
	Retina	Total retinal thickness (µm)	91.2 ± 7.75	238 ± 25.7
		Inner nuclear layer thickness (µm)	20.7 ± 2.77	46.0 ± 1.75
		Inner nuclear layer row	4 – 7	6 – 8
		Outer nuclear layer thickness (µm)	5.25 ± 1.61	43.0 ± 2.36
		Outer nuclear layer row	1 – 2	6 – 8

greater power at the cost of greater vulnerability to spherical aberrations. Direct measurements of refractive indices and power are needed to evaluate these trade-offs. The difference in lens shape should also be interpreted with caution. Because all specimens in our study were collected post-mortem, differences in lens shape might stem from differential axial shrinkage, which would disproportionately affect smaller-eyed species such as *A. crassicaudatus* compared with *S. nebulatus*. In our sections, the eye of *A. crassicaudatus* (Fig. 4A) appeared more compressed axially compared with that of *S. nebulatus* (Fig. 4B).

The retinal characteristics were consistent with those observed in various other snakes (Caprette, 2005; Hauzman *et al.*, 2014, 2017; Hauzman, 2020). The photoreceptors observed in both species were generally consistent with the types described by Underwood (1970). However, because their identification was based solely on light microscopy, the presence of double cones in *S. nebulatus* could not be unequivocally confirmed. The two species differed markedly in the thickness of the outer nuclear layer (Onl), which was thin (1–2 rows) in *A. crassicaudatus* and thick (6–8 rows) in *S. nebulatus* (Table 1). The Onl houses the nuclei of photoreceptors; therefore, a thicker Onl generally reflects a greater number of photoreceptors, greater photoreceptor convergence, and increased photosensitivity under dim-light conditions (Hauzman *et al.*, 2017). Accordingly, the thick Onl observed in *S. nebulatus* is consistent with previous studies for 11 nocturnal colubrids and may facilitate the detection of prey and predators in vegetation at night (Hauzman *et al.*, 2017; Hauzman, 2020). In contrast, despite also being nocturnal, *A. crassicaudatus* exhibited a remarkably thin Onl. This finding is inconsistent with the greater Onl thickness observed in nocturnal versus diurnal colubrids reported in Hauzman *et al.* (2017). However, this

finding appears consistent with quantitative retinal data reported by Hauzman (2014) for the congeneric *Atractus reticulatus*, which differed markedly from other nocturnal dipsadines examined, such as *Dipsas bucephala*, *Oxyrhopus guibei*, and *Sibynomorphus mikanii*. Specifically, *A. reticulatus* displayed the lowest mean photoreceptor density and rod density among all nocturnal species, a photoreceptor-to-ganglion cell convergence ratio below that of any other nocturnal species, and a ganglion cell density within the range of diurnal species (Hauzman, 2014). These data suggest that a reduced Onl may be characteristic of the genus *Atractus* rather than an anomaly of a single species, and that the thin Onl we observed in *A. crassicaudatus* reflects a retinal organization shaped by its fossorial ecology rather than diel activity alone. As a fossorial species, *A. crassicaudatus* likely relies less on visual information and more on chemical and tactile cues while moving and foraging underground, where light availability is extremely limited (Walls, 1940). In contrast, the arboreal *S. nebulatus* depends on vision to navigate vegetation and detect prey under nocturnal light conditions, where a rod-dense retina would remain advantageous. These observations suggest that retinal organization may vary with lifestyle, in addition to diel activity, and this axis of variation deserves further investigation.

Conclusion

In sum, we explored the anatomical features of the eye in two nocturnal species of dipsadine snakes with different lifestyles. These species share an overall ocular blueprint similar to that of other vertebrates (Wyneken, 2012) with little interspecific variation (Walls, 1942; Underwood, 1970) yet differ predictably in multiple traits associated with fossorial versus arboreal habits. *A. crassicaudatus* has a small eye, a thin cornea, a subspherical lens, and a thin outer layer of nuclei in the retina, features likely associated with a fossorial lifestyle. *S. nebulatus* has a large eye, a thick cornea, a spherical lens, and a thick outer layer of nuclei in the retina, features associated with an arboreal lifestyle. In conclusion, there are differences in eye anatomy among snake species of the family Colubridae, particularly within Dipsadinae, which may be associated with variation in their natural history, such as their lifestyle. This study highlights the need for additional studies that integrate morphological, ecological, functional, and evolutionary approaches.

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