Evolution, 2026, **80**(**5**), 1092–1101
https://doi.org/10.1093/evolut/qpag025
Advance access publication 14 February 2026
Brief Communication

Embryology reveals a morphological signature of ancestral diurnality maintained in a nocturnal lineage

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Abstract

Evolutionary transitions to diurnality are often associated with specialized ocular morphology, such as pits (foveae) in the retina. Foveae are required for high visual acuity and are found primarily in diurnal vertebrate taxa, including lizards. Geckos have undergone repeated evolutionary transitions between nocturnality and diurnality. *Aristelliger* is a nocturnal lineage embedded within a largely diurnal clade and represents a putative reversal to nocturnality. We investigated eye development and morphology of *Aristelliger* geckos. Despite sharing a most recent common ancestor with its diurnal sister lineage over 60 million years ago, *Aristelliger* exhibits a fovea. Fovea development is coordinated by dynamic changes in eye shape—such as ocular elongation and retraction—during embryonic development. In *Aristelliger* embryos, these elongation and retraction phases occur in the same region where the fovea forms, closely resembling the pattern seen in *Anolis*, a diurnal lizard with two foveae. Given the retention of a fovea in *Aristelliger*, we hypothesize that the transition to nocturnality is relatively recent. Incorporating these results into comparative phylogenetic methods results in a hypothesized diurnal ancestral temporal niche for sphaerodactylid geckos. We illustrate, similar to some nocturnal primates, that developmental data and robust morphological investigation can provide unique insights into macroevolutionary studies.

Keywords: embryology, eye, fovea, Gekkota, Sphaerodactylidae, retina

Introduction

Ancestral character reconstruction (ACR) is an important tool for evolutionary hypothesis testing, but ancestral states can be unclear depending on taxon sampling, node support, models of evolution, and available character state data (Omland, 1999; Schultz et al., 1996). In systems where ancestral states are unclear, developmental data can be used to provide support for certain character states (Griffin et al., 2022; Laurin & Germain, 2011; Organ et al., 2015). The evolution of new temporal niches (i.e., diel activity), such as diurnal or nocturnal activity, is often associated with major morphological changes (Röll, 2001a). Although turnover in diel activity is generally considered to have been rare throughout tetrapod evolutionary history (Anderson & Wiens, 2017), several lineages of squamate reptiles exhibit transitions between nocturnal and diurnal activity (Gamble et al., 2015; Slavenko et al., 2022; Walls, 1942). Gecko lizards (infraorder Gekkota) exemplify an ideal system to study these transitions. Geckos are hypothesized to have been ancestrally nocturnal, with at least 10 reversals to diurnality, and several tertiary transitions to nocturnality (Anderson & Wiens, 2017; Gamble et al., 2015; Pinto et al., 2019); however, the ancestral states of several lineages remain unclear. Gamble et al.'s (2015) investigation into temporal niche evolution yielded high-confidence ancestral states for most gecko families, with the exception of the Sphaerodactylidae. Sphaerodactylid geckos are a clade of predominantly diurnal geckos with a distribution spanning western Asia, the Mediterranean, northern Africa, and the tropical and subtropical regions of the Americas (Gamble et al., 2008, 2015). The majority of diurnal taxa in this family belong the "sphaerodactyl" clade (*Sphaerodactylus*, *Pseudogonatodes*, *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, and *Chatogekko*). Additional diurnal lineages in this family include *Quedenfeldtia* and *Pristurus*, while the remainder are nocturnal (*Saurodactylus fasciatus* clade, *Saurodactylus brosseti* clade, *Teratoscincus*, *Euleptes*, and *Aristelliger*). The ancestral diel activity of the most recent common ancestor (MRCA) of the Sphaerodactylidae remains uncertain, requiring either a more fully resolved phylogenetic hypothesis or

Received November 4, 2025; revisions received February 3, 2026; accepted February 12, 2026
Associate Editor: Violaine Llaurens; Handling Editor: Hélène Morlon

additional independent evidence for diel activity transitions. Studying the development of morphological features associated with diel activities can provide these critical lines of evidence to infer ancestral diel activities.

Morphological features associated with diurnal activity in geckos include sexual dichromatism and visual signaling cues (Arnold, 1993; Kabir et al., 2019, 2020; Regalado, 2012), subcutaneous or visceral hyperpigmentation (Griffing et al., 2020), round pupils (Roth et al., 2009; Underwood, 1954), retinal oil droplets (Walls, 1942; Röll, 2000), and retinal foveae (Röll, 2001b; Underwood, 1951, 1970). Foveae are photoreceptor-dense pits in the retina that are crucial for high-acuity and binocular vision (Pumphrey, 1948; Röll, 2001b; Slonaker, 1897; Walls, 1942). This specialized retinal structure is present primarily in diurnal species of teleost fish, birds, lepidosaurs, and mammals (Walls, 1942). During embryonic development, the regions that give rise to the fovea undergo temporal changes in ocular morphology—initially elongating and then later retracting. As the eye retracts, the retina remodels, condensing photoreceptors within the developing pit (Rasys et al., 2021, 2023, 2025). Geckos that have foveae typically exhibit them in the temporal region of the retina (Röll, 2001b; Underwood, 1970; Walls, 1942). These patterns of ocular morphology typically occur during mid and late development, respectively (Rasys et al., 2021, 2023, 2025) and are easily visualized in developing embryos, particularly the temporal region in foveated geckos (Griffing et al., 2020; Guerra-Fuentes et al., 2014; Rasys et al., 2021; Sandoval-Jaimes & Ramírez-Pinilla 2024). Foveae have been identified in all diurnal sphaerodactylid taxa thus far investigated (Guerra-Fuentes et al., 2014; Röll, 2001b; Underwood, 1954). However, Underwood (1970) also described a shallow fovea in the retina of the nocturnal *Aristelliger cochranae*, while noting its absence in its close relative *Aristelliger praesignis*.

The genus *Aristelliger*, commonly known as croaking geckos, is comprised of nine species of Caribbean gecko (Uetz et al., 2025). This genus exhibits vertical pupils typical of nocturnal geckos and has been consistently characterized as nocturnal and occasionally as crepuscular (Hecht, 1952; Henderson & Powell, 2009; López-Victoria & Daza, 2015; Noble & Klingel, 1932; Torres et al., 2014; Underwood, 1954). *Aristelliger* diverged from its diurnal sister lineage, *Quedenfeldtia*, approximately 70 million years ago (Gamble et al., 2008, 2011, 2015; Zheng & Wiens, 2016). Similar to sphaerodactylids as a whole, the ancestral diel activity for the MRCA of *Aristelliger* and *Quedenfeldtia* remains uncertain (Gamble et al., 2015). Herein, using opportunistic sampling of embryonic and adult morphology, we find evidence that the ancestor of *Aristelliger* was ancestrally diurnal. This newly hypothesized ancestral condition for the MRCA of *Aristelliger* and *Quedenfeldtia* shifts the probability that the ancestor of all sphaerodactylids was diurnal.

Materials and methods

We opportunistically field-collected embryos of *Aristelliger barbouri* and *A. praesignis* from Great Inagua, Bahamas, and Saint Andrew Parish, Jamaica, respectively. These species span both major clades of *Aristelliger* (Griffing et al., 2025; Keating et al., 2020). We collected two *A. barbouri* eggs during July 2015 (collecting permit issued by the Bahamas Environment, Science & Technology [BEST] Commission) and six *A. praesignis* eggs in May and June 2016 (Permit #18/27 issued by the Jamaican National Environment & Planning Agency [NEPA]). We collected specimens using protocols approved by the Institutional Animal Care and Use Committee (IACUC) of Villanova University (Protocol 5/19/15). We identified eggs as belonging to *Aristelliger* by their presence in typical habitat, digit morphology of late-stage embryos, and egg characteristics—*Aristelliger* are the only lizards on Great Inagua or Jamaica that exhibit hard-shelled eggs that are adhered to a substrate (Grant, 1940; Noble & Klingel, 1932). After removing eggs from substrate, we gently cracked their shells and submerged them in 4% neutral-buffered formalin overnight before postfixing in 70% ethanol. We visualized and photographed embryos using a Nikon SMZ1000 stereomicroscope at Villanova University and assigned developmental stages following the staging criteria of Griffing et al. (2019). Based on this staging criteria, we identified stages 33 and 43 from the *A. barbouri* eggs and stages 32, 37, 41, 42, and 43 from the *A. praesignis* eggs. The stage 43 *A. barbouri* and stage 32 *A. praesignis* embryos were damaged and were not used to examine eye morphology. The remaining opportunistically sampled embryos exhibited two undamaged eyes.

To qualitatively compare eye morphology of embryonic *Aristelliger* specimens with additional gecko material, we collected embryos from captive colonies of *Sphaerodactylus macrolepis* (diurnal sphaerodactylid), *Lepidodactylus lugubris* (nocturnal gekkonid), and *Phelsuma laticauda* (diurnal gekkonid) at Marquette University. We also compared morphology with embryos of the double-foveated, diurnal lizard *Anolis sagrei* from captive colonies at Princeton University. Husbandry, breeding, and maintenance of all species were approved by the Institutional Animal Care and Use Committees of Marquette University (IACUC; protocols MU-4192 and MU-4241) and Princeton University IACUC (protocol 2104). We removed fresh embryos from gecko and *A. sagrei* eggs following Griffing et al. (2018) and Sanger et al. (2008) protocols. Finally, we visualized and photographed embryos using a Nikon SMZ 74ST stereoscope and a Leica M205 FA stereoscope at Marquette University and Princeton University, respectively.

To characterize the histology of the *Aristelliger* retina, we collected eyes from a captive-born adult *Aristelliger lar*. After the specimen was humanely sacrificed for another study (Griffing et al., 2025), we removed both eyes ($N = 2$) and fixed them in Bouin's fixative for 48 hr before washing in 1X phosphate buffered saline (PBS) and storing in 70% ethanol. Prior to sectioning, we dehydrated eyes in increasing serial ethanol dilutions, treated with xylene, and embedded in paraffin. Finally, we cut the tissue into horizontal sections (10 µm thick) using a Leica RM2235 microtome and mounted them on slides prior to performing immunofluorescence and hematoxylin and eosin (H&E) staining.

For immunofluorescence, we deparaffinized slides in xylene and rehydrated in decreasing ethanol dilutions. We performed antigen retrieval in sodium citrate buffer at 90 °C for 30 min. Slides were then washed in PBS, permeabilized, and blocked in 0.5% Triton and 10% sheep serum in PBS for 1 hr. After washing, we incubated slides for 1 hr in a primary antibody solution of 1:100 mouse-anti-glutamine synthetase (Millipore MAB302) and 1:500 rabbit-anti-RG opsin (Millipore AB5405) in PBS. Glutamine synthetase labels Müller glia—the primary glial cell type in the retina. RG opsin labels both red and green cone opsins—the G-protein-coupled receptors involved in green and red light perception. We then washed slides in PBS and incubated them in a 1:1000 secondary antibody solution in PBS overnight at 4 °C in a humid chamber. Finally, we washed slides in PBS, mounted with Fluoromount G (Invitrogen), and imaged with a Zeiss 700 confocal microscope at the National Eye Institute (NEI) imaging core at the National Institutes of Health. After removing coverslips, we stained sections in Gill no. 2 hematoxylin (Sigma-Aldrich) for 10 min, rinsed, stained with eosin Y for 10 min, and rinsed again. We then dehydrated slides in increasing serial ethanol dilutions, treated with xylene, and mounted, this time using Cytoseal XYL (Thermo) before cover-slipping and imaging with a Zeiss Z2 imager at the NEI imaging core.

We collected measurements from horizontal histological sections using FIJI (Schindelin et al., 2012). We measured the thickness of all retinal layers, and then the individual nuclear layers: the ganglion cell (GCL), inner nuclear (INL), and outer nuclear layers (ONL). We then calculated the ratio of each nuclear layer to the total retinal thickness. We collected thickness measurements for five technical replicates per retina region (nasal, central, and fovea). We also measured photoreceptor density from horizontal histological sections using FIJI. We measured the area of the total retina and counted nuclei in the ONL. We collected density measurements for three technical replicates per retina region. Finally, we compared differences between thickness ratio and photoreceptor density measurements in the different regions using two-tailed *t*-tests (Supplemental Materials 1 and 2).

Using the diel activity data and phylogeny from Gamble et al. (2015), we performed discrete ACRs in R (v4.4.2; R Core Team, 2024) with the packages ape (Paradis & Schliep, 2019) and phytools (Revell, 2024), following the methodology of Revell and Harmon (2022). Briefly, using phylogeny and character states of Gamble et al. (2015), we performed ACRs using both the complete taxon sampling (total tree) and a sampling pruned to include only sphaerodactylid taxa ($N = 50$; pruned tree) using the function “drop.tip.” We identified an equal rates (ER) model and an all rates different (ARD) model as the best fitting models of evolution for the pruned tree and total tree, respectively, using the R package geiger (Pennell et al., 2014; Supplementary Material 3). We then performed stochastic character mapping, simulating 100 trees under an ER model for the pruned tree and an ARD model for the total tree using the function “make.simmap.” We performed ACRs under two scenarios: (1) using the same character states as Gamble et al. (2015), where members of the genus *Aristelliger* are coded as nocturnal, and (2) where the MRCA of *Aristelliger* and its sister lineage *Quedenfeldtia* is coded as diurnal using the function “bind.tip.”

Results

Embryos representing mid- and late-developmental stages were collected from several *Aristelliger* geckos for comparative analysis. Upon examining field-collected embryos from *Aristelliger barbouri* (stage 33) and *A. praesignis* (stages 37 and 41), we found that early–mid postovipositional stages (stages 33 and 37) exhibited temporal elongation of the eye (Figure 1A–D). In contrast, the single late postovipositional stage (stage 41) of *A. praesignis* did not display an elongated temporal region of the eye (Figure 1E–F). To compare these patterns of eye development, we examined stage 33, 37, and 41 specimens of one bifoveated iguanian lizard (*Anolis sagrei*; Figure 2A–C), two foveated geckos (*Phelsuma laticauda* and *Sphaerodactylus macrolepis*; Figure 2D–I), and two non-foveated geckos (*Lepidodactylus lugubris* and *Correlophus ciliatus*; Figure 2J–O). In *Anolis sagrei*, temporal ocular elongation is evident at stage 37 (Figure 2B) and then recedes by stage 41 (Figure 2C). Similarly, both *P. laticauda* and *S. macrolepis* show temporal ocular elongation at stages 33 and 37 (Figure 2D–E, G–H), followed by subsequent retraction by stage 41 (Figure 2F, I). As expected, none of the sampled developmental stages for *L. lugubris* or *C. ciliatus* showed evidence of temporal ocular elongation or retraction, and eye shape remained relatively constant (Figure 2J–O). Collectively, the developmental evidence suggests that *Aristelliger* undergoes dynamic temporal ocular shape changes, also indicating the presence of a potential temporal fovea.

To investigate this further, we histologically characterized the retina of an adult *Aristelliger lar* (Figure 3A–G). Within the temporal retina, we identified a small, shallow pit marked by elevated photoreceptor density and a thinning caused by the lateral displacement of both the INL and GCL (Figure 3A inset, D). In comparison, the nasal and central retinal regions exhibit a uniform, single-layered photoreceptor arrangement with no displacement of inner retinal layers (Figure 3B–C, E–F). Additionally, photoreceptors in the temporal pit possess morphological features characteristic of foveated retinas, including elongated processes and narrower inner and outer segments, compared to the broader and thicker segments observed in non-foveated regions (Figure 3E, G). The relative thickness of individual nuclear layers was not significantly different between the nasal, central, and fovea regions, with three exceptions: the central inner nuclear layer is significantly thicker than the nasal inner nuclear layer, and the fovea ONL is significantly thicker than both the nasal and central nuclear layers (Figure 3H; Supplemental Material 1). The density of cells within this ONL is significantly higher in the fovea region than the nasal or central regions (Figure 3I; Supplemental Material 2). Together, these findings indicate that adult *Aristelliger* possess a shallow temporal fovea and suggest that the lineage was likely ancestrally diurnal.

To examine the effect of changing the ancestral diel activity state of *Aristelliger* in a macroevolutionary context, we performed ACRs using data from Gamble et al. (2015). Delta-Akaike Information Criterion between the two scenarios is <2 (Supplemental Material 3). For scenario 1 using the pruned tree, there were 6.04 average changes from diurnal to nocturnal and 1.83 changes from nocturnal to diurnal (Supplemental Material 4). The probability that nodes were diurnal for the MRCA of *Aristelliger* and *Quedenfeldtia*, the MRCA of the clade containing *Aristelliger*, *Quedenfeldtia*, *Euleptes*, *Saurodactylus fasciatus* clade, and *Teratoscincus*, and the MRCA of all sphaerodactylids was 0.45, 0.45, and 0.67, respectively (Figure 4A; Supplemental Materials 5, 6). For scenario 2 using the pruned tree, there were 7.54 average changes from diurnal to nocturnal and 0.71 changes from nocturnal to diurnal (Supplemental Material 4). The probability that the node for the MRCA of

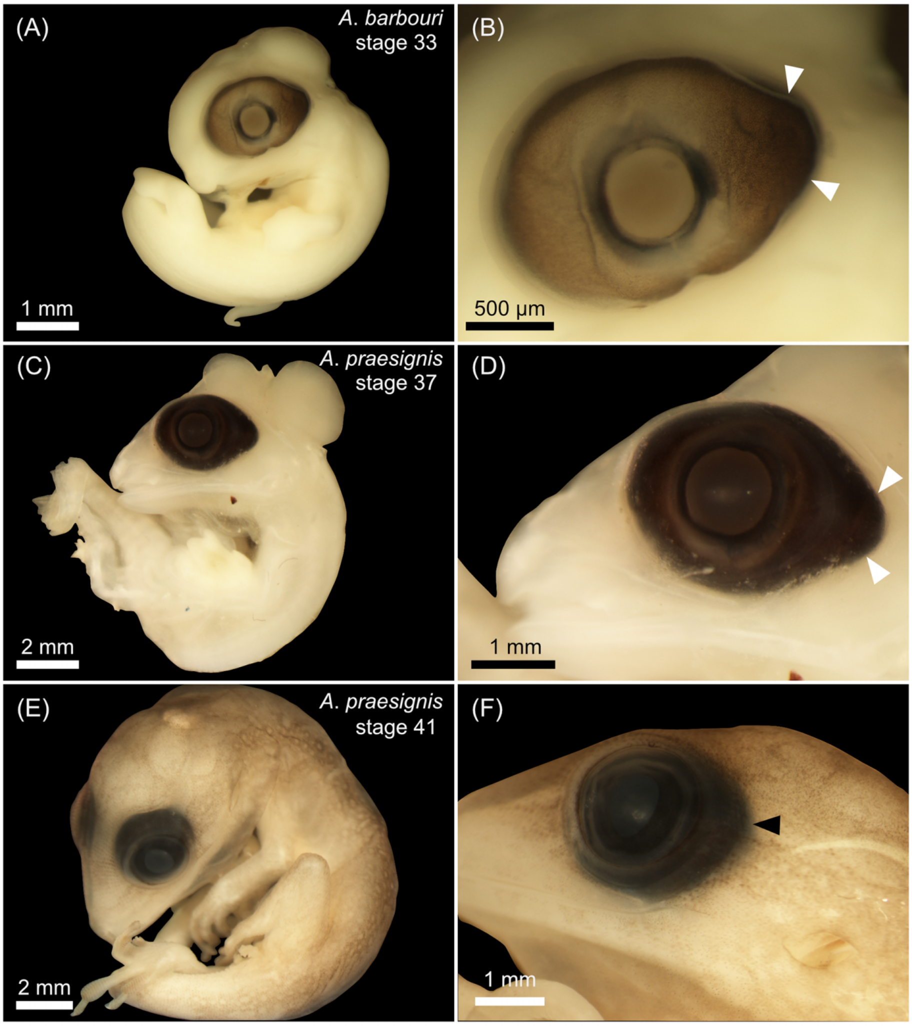

Figure 1. Field-collected, formalin-preserved embryonic specimens of *Aristelliger*. (A) Lateral view of a stage 33 *Aristelliger barbouri* embryo (AMB 9353). (B) Magnified view of the ovoid eye of AMB 9353 exhibit posterior extension of the RPE. (C) Lateral view of a stage 37 *Aristelliger praesignis* embryo (MCZ A-36038). (D) Magnified view of the ovoid eye of MCZ A-36038 exhibit posterior extension of the RPE. (E) Lateral view of a stage 41 *Aristelliger praesignis* embryo (MCZ A-28982). (F) Magnified view of eye of MCZ A-28982 without obvious extension of the RPE. White arrows point toward temporal extension of the RPE. Black arrows signify retraction of the RPE.

Aristelliger and *Quedenfeldtia* was forced to be 1.00 for the scenario. The probability that nodes were diurnal for the MRCA of the clade containing *Aristelliger*, *Quedenfeldtia*, *Euleptes*, *Saurodactylus fasciatus* clade, and *Teratoscincus*, and the MRCA of all sphaerodactylids was 0.91, and 0.77, respectively (Figure 4B; Supplemental Materials 5, 6). Summaries of the ACRs using the total tree can be found in Supplemental Materials 4–8.

Discussion

Our developmental and histological analyses both demonstrate that species of the nocturnal gecko genus *Aristelliger* possess a temporal fovea (Figures 1 and 3). This specialized retinal structure is associated with high acuity vision, binocular vision, and ultimately, diurnal activity (Pumphrey, 1948; Röll, 2001b; Slonaker, 1897; Walls, 1942). The embryonic eye morphology of *Aristelliger* more closely resembles that of diurnal lizards during early development, such as *Phelsuma laticauda* and *Anolis sagrei*, than that of nocturnal lizards (Figure 2). The ocular elongation and retraction, seen in both our sample of *Aristelliger* embryos and diurnal lizard embryos, is a process that condenses photoreceptors in the area that will become the fovea (Rasys et al., 2021, 2023, 2025). Our histological data confirms that the fully developed *Aristelliger* fovea exhibits a denser layer of photoreceptors than other portions of the retina. Although the fully developed fovea of an adult *Aristelliger* exhibits the characteristic concave morphology and enrichment for photoreceptors (Figure 3), it is extraordinarily shallow when compared to other diurnal lizards, including *A. sagrei*, *Chamaeleo calyptratus*, and *Lygodactylus kimhowelli* (Rasys et al., 2021, 2023); however, bares resemblance to the shallow fovea of the diurnal *P. laticauda* (Wegerski et al., 2024). This inconspicuous morphology may explain why Underwood's (1970) investigation of the *Aristelliger praesignis* retina was unable to identify a fovea. The shallow nature of the *Aristelliger* fovea could suggest a diminished capacity for funneling light when compared with other diurnal taxa. However, functional experiments are needed to

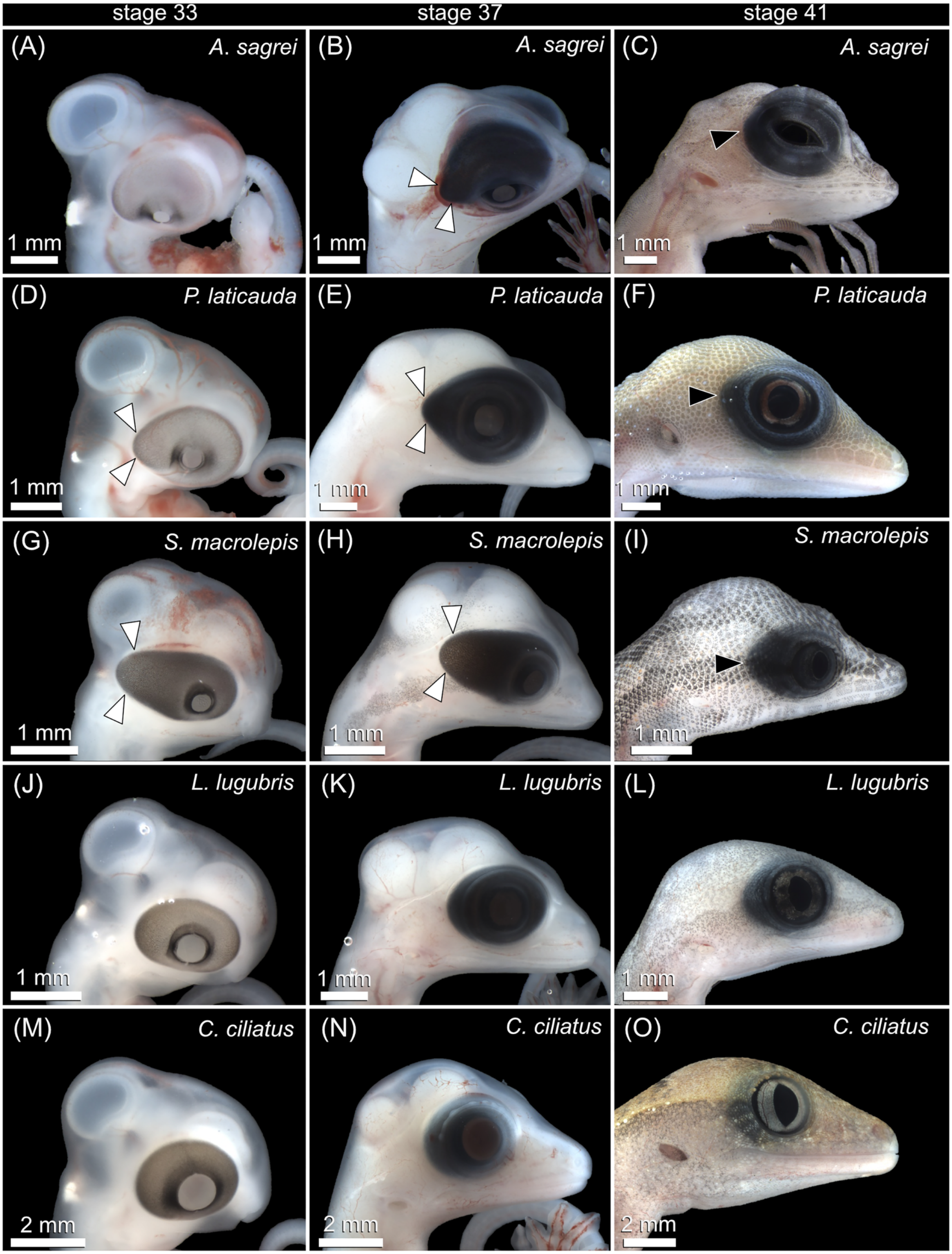

Figure 2. Embryonic eye morphology in five species of lizard. Lateral view of the crania of the diurnal iguanian *Anolis sagrei* (A–C), the diurnal gekkotans *Phelsuma laticauda* (D–F) and *Sphaerodactylus macrolepis* (G–I), and the nocturnal gekkotans *Lepidodactylus lugubris* (J–L) and *Correlophus ciliatus* (M–O). Each row illustrates embryonic stages 33 (A, D, G, J, M), 37 (B, E, H, K, N), and 41 (C, F, I, L, O). White arrows point toward temporal extension of the RPE. Black arrows signify retraction of the RPE.

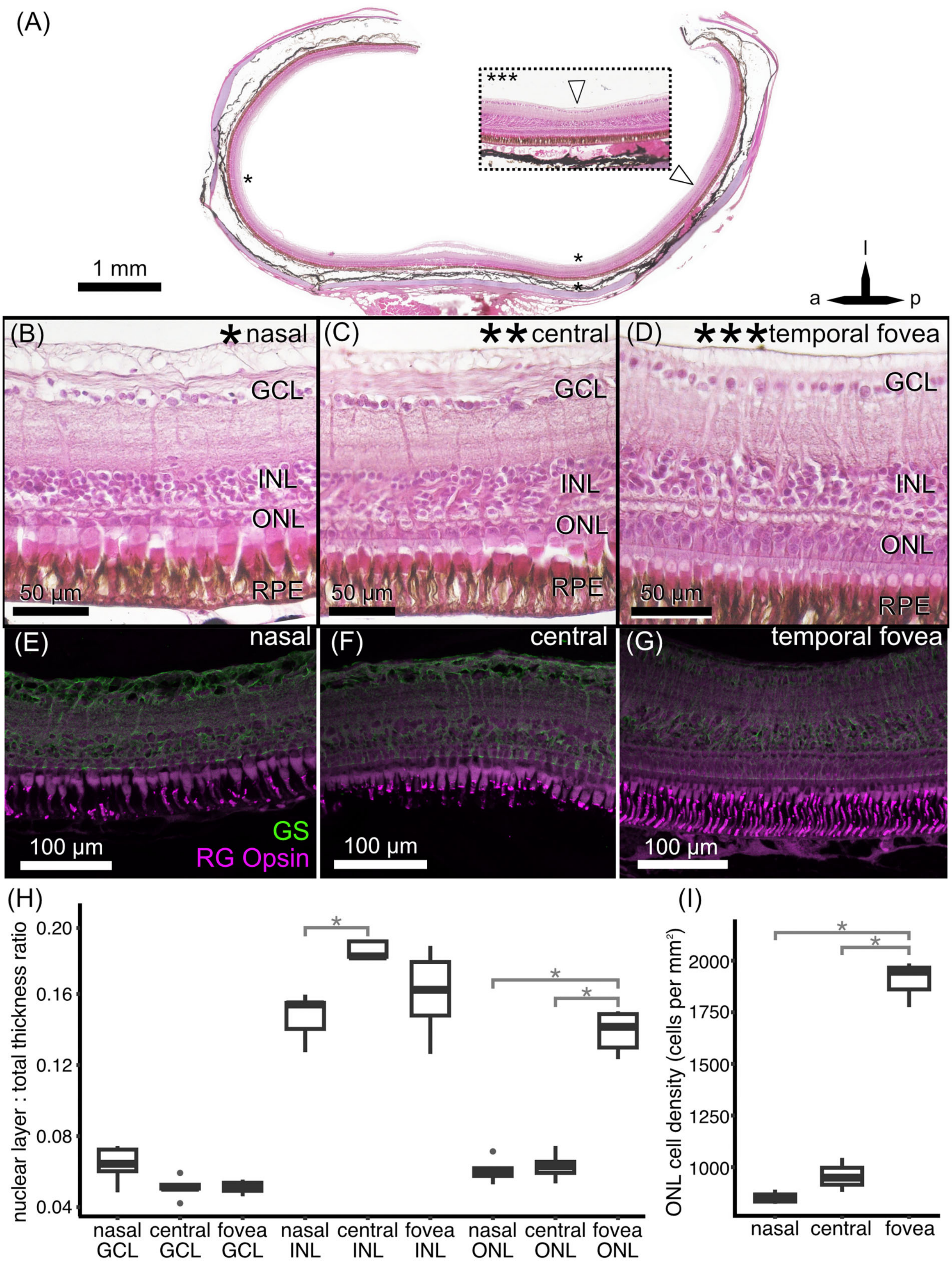

Figure 3. Histology of the retina of an adult *Aristelliger lar*. (A–D) Hematoxylin and eosin stained horizontal sections of the eye with magnified views of the nasal (B), central (C), and temporal fovea (D) regions of the retina. White arrows point toward temporal fovea. a, anterior; l, lateral; p, posterior; GCL, ganglion cell layer; INL, inner nuclear layer; ONL, outer nuclear layer; RPE, retinal pigmented epithelium. (E–G) Immunofluorescence of glutamine synthetase (GS; green) and red/green (RG) opsin (magenta) in the nasal (E), central (F), and temporal fovea (G) regions of the retina. (H) Thickness ratios of individual nuclear layers to the total thickness of the retina in the nasal, central, and fovea regions of the retina. All comparisons between different regions of the retina were not significantly different except nasal INL vs. central INL (*p*-value = .002), nasal ONL vs. fovea ONL (*p*-value = 8.36 e10^{-6}), and central ONL vs. fovea ONL (*p*-value = 6.96 e^{-6}). (I) ONL cell density (cells per mm^2) in the nasal, central, and fovea regions of the retina. Nasal vs. fovea region (*p*-value = .002) and central vs. fovea region (*p*-value = .001) were significantly different.

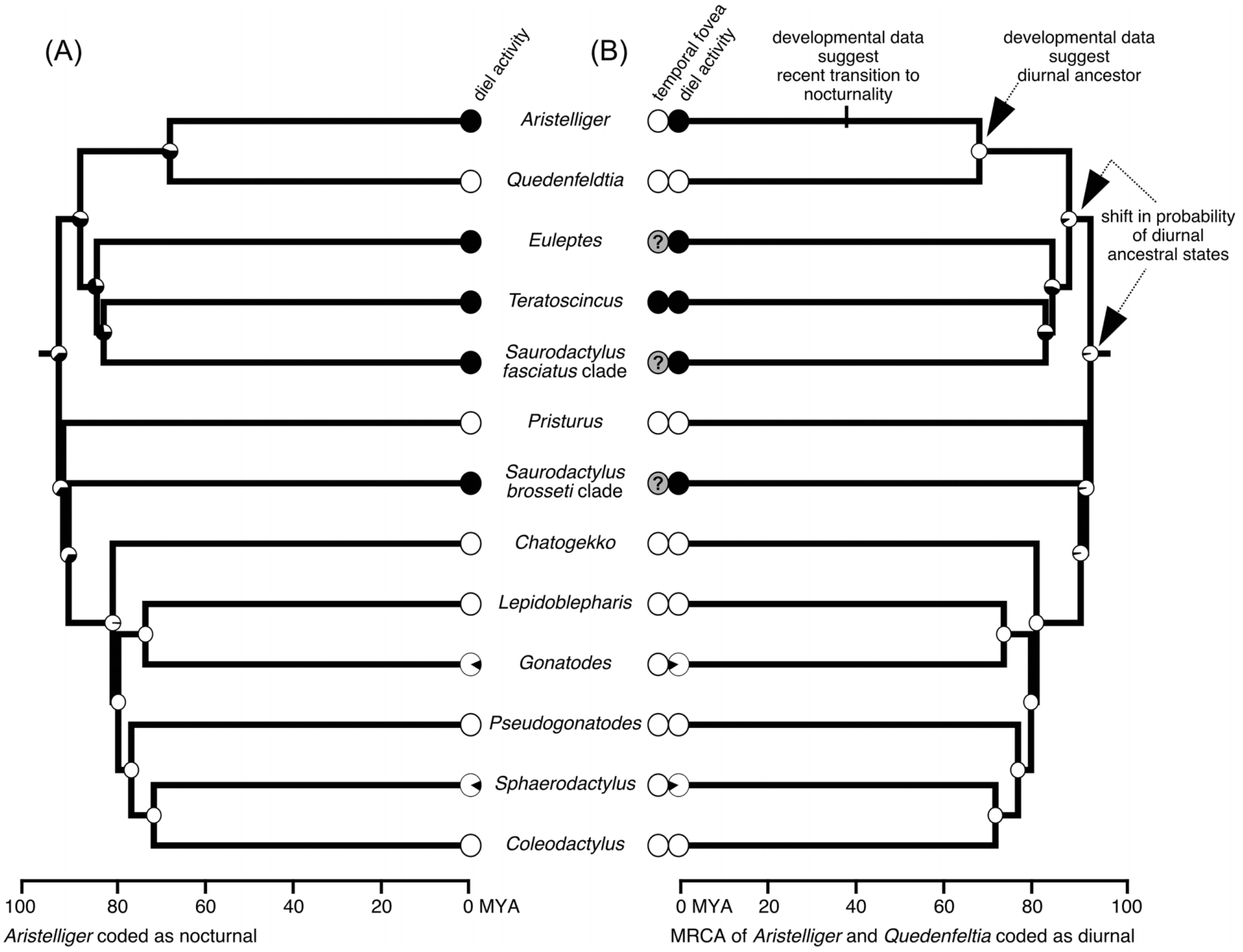

Figure 4. Hypothesized diel activity evolution and ancestral character reconstruction (ACR) in sphaerodactylid geckos. (A) ACR with diel activity character states recapitulates the hypothesis of Gamble et al. (2015). (B) ACR with the most recent common ancestor (MRCA) of *Aristelliger* and *Quedenfeldtia* coded as diurnal results in a shift in probability that ancestral sphaerodactylids were diurnal. Time-calibrated phylogeny and diel activity data from Gamble et al. (2015). Circles at the tips of branches indicate diel activity as diurnal (white) or nocturnal (black). Predominantly white circles with black slivers correspond to *Sphaerodactylus* and *Gonatodes*, which exhibit some secondarily nocturnal species. The additional column of circles at the tips of (B) indicates the presence (white) or absence (black) of temporal fovea. Fovea data from Underwood (1951, 1954, 1970) and Röll (2001b). Gray circles illustrate lineages in which the presence of a fovea is unknown. Scale corresponds to millions of years (MYA). The genus *Saurodactylus* is consistently reported as polyphyletic (Gamble et al., 2015; Rato & Harris, 2008).

determine if a fovea of this shallow morphology can reduce light scattering like diurnal lizards. In addition to the fovea we describe, *Aristelliger* has been reported to possess colorless photoreceptor cell oil droplets in their retina (Röll, 2000; Underwood, 1951), structures implicated in light filtering and spectral tuning (Bowmaker & Knowles, 1977). Taken together, we posit that *Aristelliger* evolved nocturnality relatively recently and that the MRCA with its sister lineage, the diurnal *Quedenfeldtia* geckos, was diurnal.

The character state of the MRCA of sphaerodactylids was uncertain in Gamble et al.'s (2015) analysis of diel activity evolution in geckos. The MRCA of sphaerodactylids was recovered as either nocturnal, diurnal, or crepuscular/cathemeral depending on the method of ACR. In our analysis, by either coding species in the genus *Aristelliger* or the node representing the MRCA of *Aristelliger* and *Quedenfeldtia* as diurnal, we increased the probability that the ancestral state of sphaerodactylids was diurnal from 0.67 to as high at 0.97, suggesting that the Sphaerodactylidae is ancestrally diurnal (Figure 4; Supplementary Materials 5 and 6). This would suggest that *Aristelliger*, *Teratoscincus*, *Euleptes*, *Saurodactylus fasciatus*, and the *Saurodactyous brosseti* clade are all tertiarily nocturnal. In addition to these new insights on gecko temporal niche evolution, our results demonstrate that seemingly small changes to the input character states can create major shifts in ACR estimations.

The persistence of a temporal fovea in *Aristelliger* suggests a degree of phylogenetic momentum (*sensu* Simpson, 1944). A similar pattern occurs in the nocturnal gecko *Sphaerodactylus parkeri*, which also retains a temporal fovea (Underwood, 1951) and, like most nocturnal *Sphaerodactylus*, most likely evolved nocturnality relatively recently (Gamble et al., 2015; Scantlebury et al., 2011). The nocturnal primates *Tarsius* and *Aotus* also exhibit foveae, suggesting a relatively recent shift to nocturnality (Martin & Ross, 2006; Polyak, 1957; Provis et al., 1998; Santini et al., 2015). In contrast, some geckos that are hypothesized to have recently transitioned from nocturnality to diurnality (e.g., *Aprasia*, *Delma*, *Rhoptropus*) lack a fovea (Röll, 2001b; Underwood, 1970). Despite the presence of foveae, *Aristelliger* and *S. parkeri* (as well as other more recently nocturnal geckos, such as *S. roosevelti*) exhibit vertical pupils typical of nocturnal geckos and other reptiles that are active in low-light environments (Brischoux et al., 2010; Gamble et al., 2015; Grant, 1939; Underwood, 1954). This diurnal–nocturnal mismatch in character states suggests that pupil shape evolution is more rapid than gain or loss of foveae, providing further evidence of the mosaic nature of adaptations for diurnality in geckos (Gamble et al., 2015). Because fovea formation occurs early in development, involves extensive retinal remodeling (Rasys et al., 2021, 2023, 2025), and because the eye develops in close coordination with the brain and skull, the long-term retention of foveae may reflect developmental constraint and the integration of craniofacial developmental processes. Given the frequency with which geckos have transitioned between temporal niches and the major changes in development and anatomy associated with such transitions, this lineage can provide many study systems to understand phylogenetic momentum, developmental remodeling, and ocular morphology.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data presented in this manuscript are included in the supplemental materials, or, in the case of raw image data, are uploaded to FigShare digital repository (DOI: 10.6084/m9.figshare.31173856). Phylogenetic and diurnality character data are available from the supplemental materials of Gamble et al. (2015; DOI: 10.5061/dryad.97b50).

Author contributions

A.H.G. and A.M.R. conceived and designed the study. A.H.G., A.E.W., and A.M.R. collected the data. All authors analyzed the data and edited the manuscript.

Funding

National Science Foundation DBI-2209090 to AHG, Villanova University Department of Biology to AHG and AMB, and Villanova University Gerald E. Lemole Endowed Chair Fund to AMB.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was funded, in part, by the Villanova University Department of Biology, the Villanova University Gerald E. Lemole Endowed Chair Fund, and the National Science Foundation. Field collection of *A. barbouri* and *A. praesignis* was made possible by the Bahamas National Trust and Jamaican National Environment & Planning Agency, respectively. Additionally, we thank Liam Revell and his extensive community problem-solving and documentation for phytools. We thank two anonymous reviewers for their helpful feedback on an earlier version of this manuscript.

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Received November 4, 2025; revisions received February 3, 2026; accepted February 12, 2026
Associate Editor: Violaine Llaurens; Handling Editor: Hélène Morlon