

REPORT

PALEONTOLOGY

Evolution of vision and hearing modalities in theropod dinosaurs

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Owls and nightbirds are nocturnal hunters of active prey that combine visual and hearing adaptations to overcome limits on sensory performance in low light. Such sensory innovations are unknown in nonavian theropod dinosaurs and are poorly characterized on the line that leads to birds. We investigate morphofunctional proxies of vision and hearing in living and extinct theropods and demonstrate deep evolutionary divergences of sensory modalities. Nocturnal predation evolved early in the nonavian lineage Alvarezsauridae, signaled by extreme low-light vision and increases in hearing sensitivity. The Late Cretaceous alvarezsaurid *Shuvuuia deserti* had even further specialized hearing acuity, rivaling that of today's barn owl. This combination of sensory adaptations evolved independently in dinosaurs long before the modern bird radiation and provides a notable example of convergence between dinosaurs and mammals.

Sensory specializations are some of the most distinctive vertebrate innovations (1, 2) and are common as adaptations to low-light activity in birds and mammals. Facultative nocturnal behaviors of living birds, such as tactile probing and dab-

bling in some water birds, require limited sensory anatomical changes (3). However, most nocturnal birds have conspicuous modifications of the visual system, and specialized nocturnal foragers of active prey combine adaptations of both vision and hearing (4).

Such adaptations enable distinctive foraging strategies such as the use of precise sound localization and low-light (scotopic) vision in the barn owl (*Tyto alba*), which can hunt in complete darkness (5). These sensory adaptations leave clear skeletal signatures that should be evident in fossils. Nevertheless, sensory evolution in birds and their theropod stem lineage is poorly understood [but see, e.g., (6–9)]. This is a substantial shortcoming in our understanding of dinosaurian biology and of the structure of Mesozoic ecosystems.

To evaluate the evolution of vision and hearing in extinct theropods, we studied skeletal proxies for two sensory systems: the scleral ossicle ring (hereafter “scleral ring”) of the eye for vision and the endosseous cochlear duct of the bony labyrinth for hearing. The scleral ring is embedded in the eyeball surface in numerous living and extinct amniotes. Nocturnal species typically have wider ring apertures, reflecting larger pupil sizes that increase light sensitivity (9). The endosseous cochlear duct is intimately linked to hearing performance (e.g., sensitivity and frequency range) because it houses the basilar papilla or cochlea (10). The elongate mammalian cochlea has been an area of continued evolutionary innovation [e.g., (11, 12)], demonstrating the

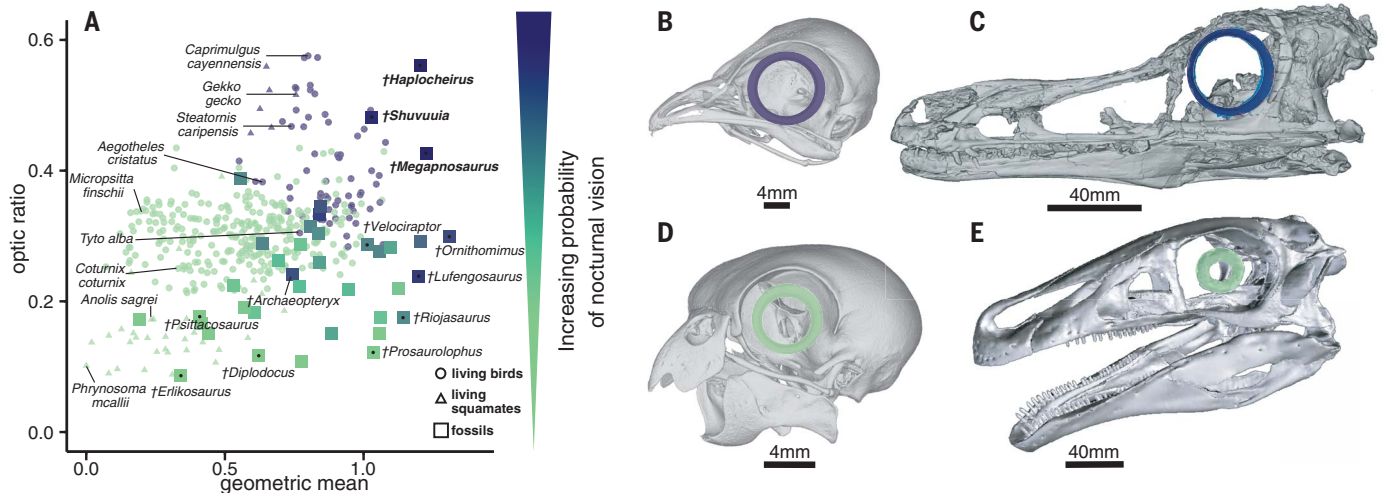


Fig. 1. Optic ratio by geometric mean of optic measurements for living birds, squamates, and nonavian theropods. (A) Scatterplot of optic ratio versus geometric mean of orbit and scleral ring measurements for extant birds and reptiles and extinct species. See data S3. (B to E) Scleral ossicle ring anatomy in (B) *Aegotheles cristatus*, (C) *H. sollers*, (D) *Micrositta finchii*, and (E) *Erlisosaurus andrewsi* (29). Blue indicates nocturnality, green indicates non-nocturnality, and color gradient indicates the posterior probability of nocturnality (data S3) (19). † indicates extinct species.

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importance of hearing in their foraging strategies. Bird species that rely on auditory cues for foraging, such as owls, have an elongate endosseous cochlear duct, alongside other anatomical modifications (13).

Our analyses show visual and auditory adaptations to nocturnality in alvarezsauroids, an enigmatic theropod lineage that spanned the Late Jurassic to Late Cretaceous. Early branching alvarezsauroids, such as *Haplocheirus sollers*, retain generalized theropod features that suggest a relatively unspecialized predatory ecology (14). However, late-branching alvarezsauroids such as *Shuvuuia deserti* have a curious mixture of derived traits, including birdlike skulls, cursorial hindlimbs, and short, functionally monodactyl forelimbs interpreted as adaptations for scratch digging (15, 16). These features are the source of continued speculation and debate about alvarezsauroid paleoecology (15–18).

Our digital reconstructions of the scleral rings of the alvarezsauroids *Haplocheirus* and *Shuvuuia* show a proportionally large eye with an extremely wide aperture (Fig. 1 and figs. S1 to S5) (19). Phylogenetic flexible discriminant analysis of the scleral ring and orbit morphology, extended from previous analyses (9), has a mean accuracy of 92.0% for the classification of extant species as nocturnal or non-nocturnal. Among theropods, the highest posterior probabilities for nocturnal vision ($pp_{\text{nocturnal}}$) are for *Haplocheirus* ($pp_{\text{nocturnal}} > 0.99$), *Shuvuuia* ($pp_{\text{nocturnal}} > 0.87$), and the coelophysoid *Megapnosaurus* ($pp_{\text{nocturnal}} > 0.99$) (Fig. 1 and table S1). These have morphologies similar to those of birds that have specialized low-light visual systems (Fig. 1) but are different from those of other theropods, including many for which nocturnality was previously inferred at a much less stringent probability threshold ($pp_{\text{nocturnal}} > pp_{\text{diurnal}}$ and $pp_{\text{cathemeral}}$) (6).

Micro-computed tomography (CT) reveals anatomical specialization of the endosseous cochlear duct in *Shuvuuia*, similar to the barn owl (*T. alba*), with large duct diameters and a proximodistally elongate morphology, curving posteromedially under the brain cavity. These anatomies are unlike those of almost all other theropods. Cochlear duct elongation imposes spatial constraints on the labyrinth in both taxa (Figs. 2 and 3), which have low, broad semicircular canals compared with their evolutionary relatives (20) (Fig. 3B). Both taxa also show two well-defined laminae that extend along the length of the endosseous cochlear duct, medially (primary bony lamina) and laterally (secondary bony lamina) (Fig. 2). Similar laminae in mammals are attachment sites for the basilar membrane, which supports the basilar papilla.

Comparison of endosseous cochlear duct length to braincase height across 88 extant

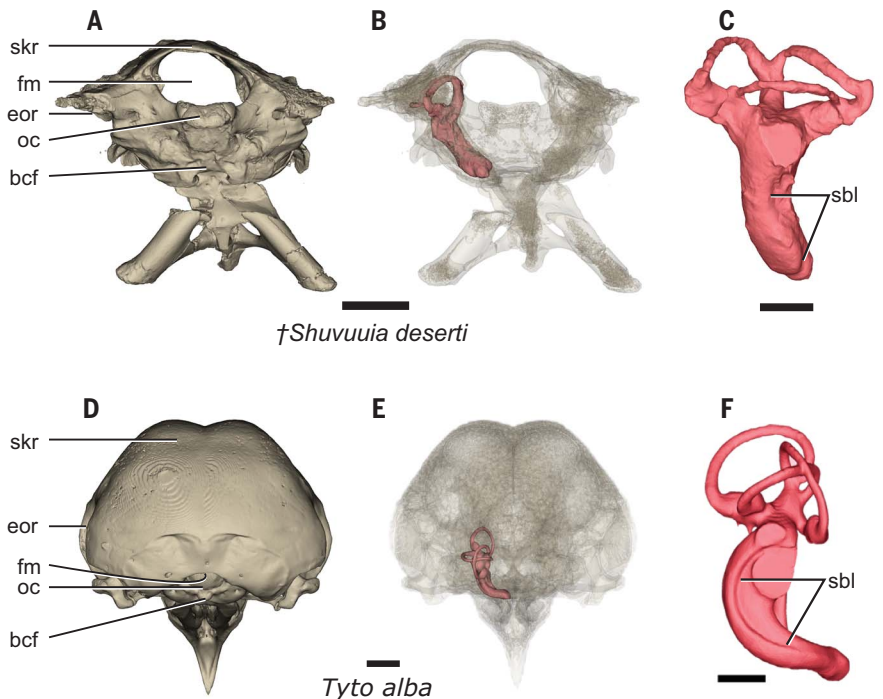


Fig. 2. Comparative anatomy of the endosseous cochlear duct of *S. deserti* (uncrushed adult specimen IGM100/1304) and the extant barn owl *T. alba*. (A to C) *S. deserti* uncrushed adult specimen (IGM100/1304). (D to F) Extant barn owl *T. alba*. (A and D) Posterior views of braincases showing external anatomy. (B and E) Transparent CT renderings of braincase in posterior view, showing endosseous labyrinths. (C and F) Digital reconstructions of the endosseous labyrinths in lateral view. Scale bars, 5 mm (B and E) and 2.5 mm (C and F). bcf, braincase floor; eor, external otic region; fm, foramen magnum; oc, occipital condyle; sbl, secondary bony lamina; skr, skull roof. † indicates extinct species.

birds corroborates our interpretation of relative duct elongation as related to nocturnality and other foraging traits (Fig. 3, table S2, and figs. S6 to S10) (19). Owls (Strigiformes); large-bodied, nocturnal Strisores (e.g., owl nightjars, potoos, frogmouths, and the echolocating oilbird); and some other taxa have moderately or greatly elongated ducts (Fig. 3), whereas vocal learners do not (fig. S6 and table S3). This suggests that duct elongation is an adaptation for auditory foraging, contradicting the hypothesis that it evolved to facilitate intraspecific communication (10). Woodpeckers, which use auditory foraging of concealed insects, show limited to moderate duct elongation (table S3). Some water-associated birds, including gannets, kingfishers, and cormorants, also show moderate duct elongation that deserves further investigation (table S3). Nightjars, which are low-light predators of aerial prey in generally open environments, show only limited duct elongation (table S3).

Elongation of the endosseous cochlear duct also occurs among Mesozoic theropods, including some predatory groups (Troodontidae, Tyrannosauridae, and Dromaeosauridae); in the

secondarily herbivorous Therizinosauria; and in alvarezsauroids, including the Jurassic to Early Cretaceous taxa *Haplocheirus* and *Xiyunykus* (Fig. 3). The barn owl (*T. alba*), *Shuvuuia*, and an undescribed troodontid [Mongolian Institute for Geology (IGM) 100/1126] are outliers that demonstrate auditory specialization, even compared with other owls, strisorans, and Mesozoic theropods (Fig. 2) (20, 21). Proportional reduction of the endosseous cochlear duct occurs in oviraptorosaurs and ornithomimosaurs, which are hypothesized to be herbivores or omnivores (22, 23).

The proportionally large eyes and scleral ring apertures of *Haplocheirus* and *Shuvuuia* indicate nocturnal visual adaptation. These represent some of the earliest and latest alvarezsauroids, suggesting that nocturnal visual capabilities were widespread in that group. The early appearance and phylogenetic retention of nocturnal visual adaptations in alvarezsauroids contrasts with inferences of equivocal or diurnal activity patterns in most other theropods, including early birds (Avialae) (Fig. 4). This distribution suggests a deep evolutionary divergence of activity patterns among theropods, with alvarezsauroids becoming nocturnal

visual specialists (Fig. 4). The hearing-related anatomy of *Shuvuuia*, comprising an exceptionally elongate endosseous cochlear duct and the presence of a secondary bony lamina, is highly

comparable to that of the barn owl among extant birds (Fig. 2) and corroborates the hypothesis of specialized nocturnal foraging in alvarezsauroids. This mode of life is rare in

birds (4), and we also find that it was rare in nonavian theropods, contrasting with the relatively high incidence of nocturnal foraging in mammals (24).

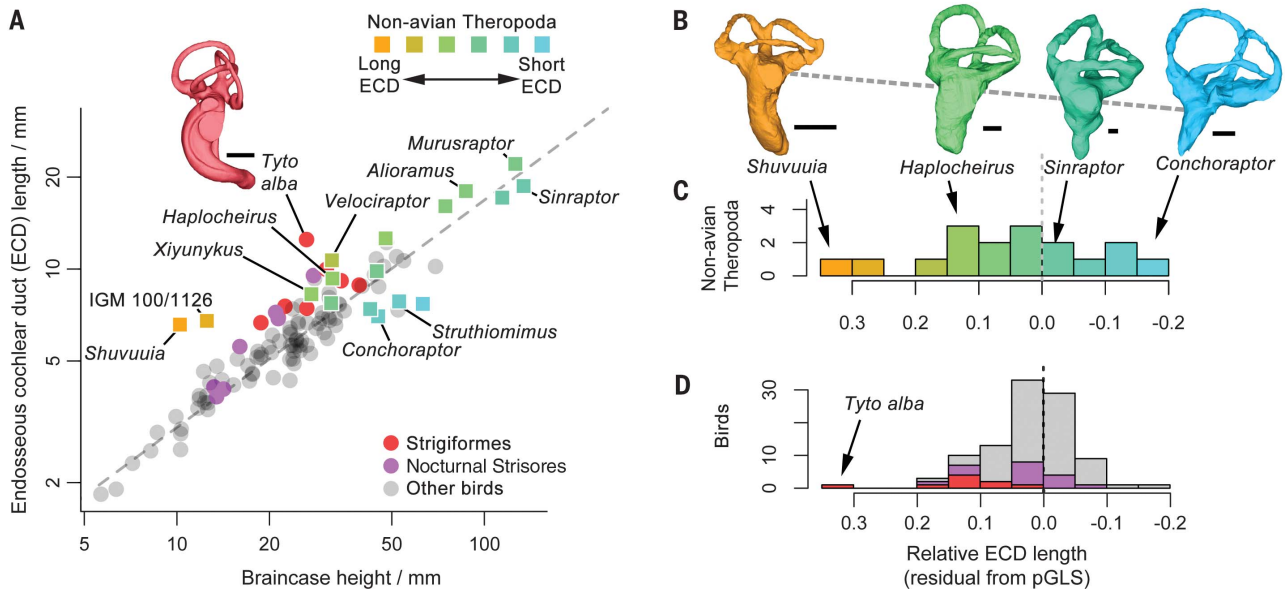


Fig. 3. Endosseous cochlear duct (ECD) length in a sample of birds and nonavian theropod dinosaurs. (A) ECD length versus braincase height for extant birds [regression line $\log_{10}(\text{ECD length}) = -0.265 + 0.744 \times \log_{10}(\text{braincase height})$; $P < 0.0001$; λ (phylogenetic signal) = 0.89; $N = 88$]. Residuals indicate relative duct length, indicated with a color gradient for nonavian theropods. (B) Endosseous labyrinths of selected nonavian theropods colored according to residual duct length. The gray line follows the fenestra ovalis. (C and D) Histograms showing relative duct lengths among sampled extant birds (C) and nonavian theropods (D). Scale bars, 2.5 mm. pGLS, phylogenetic generalized least squares regression.

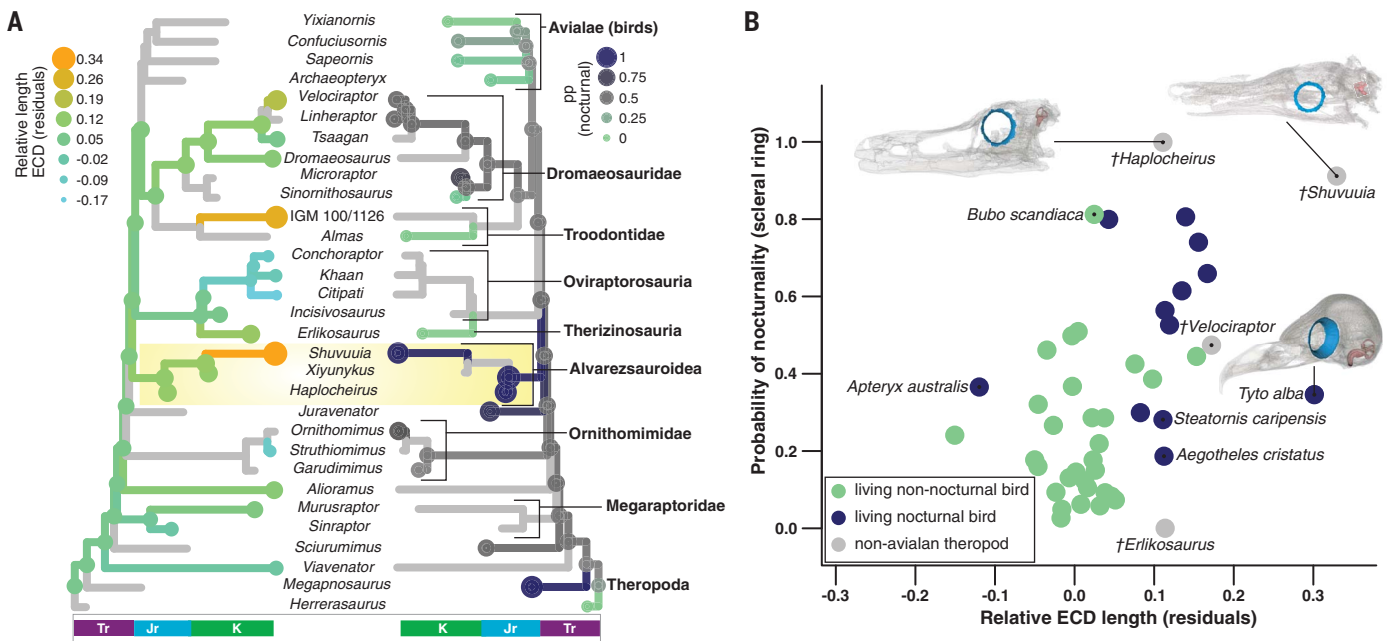


Fig. 4. ECD length residuals and $pp_{\text{nocturnal}}$ for selected theropods. (A) Phylogeny of study sample mapping duct-length residuals and posterior probability of nocturnality in Mesozoic theropods. (B) $pp_{\text{nocturnal}}$ versus relative ECD length (residuals) for extant and extinct theropods. Skulls (clockwise): *H. sollers* [Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V15988], *S. deserti* (IGM100/0977; labyrinth from IGM100/1304), and *T. alba*. See also figs. S8 and S9. † indicates extinct species.

Even moderate elongation of the endosseous cochlear duct is rare in our broad sample of extant birds (Fig. 3D). It occurs most frequently (though not exclusively) in owls and large-bodied nightbirds such as frogmouths, owl nightjars, and potoos (table S3). These are predominantly nocturnal predators of highly mobile and often cryptic, ground-based, and near-perch prey (3). Many of these taxa forage for prey items that were also available to extinct theropod dinosaurs (including terrestrial invertebrates and small vertebrates) by ground running and pouncing from a low perch (e.g., frogmouths) or descent from quartering flight (e.g., owls) (3). Increased hearing ability in these groups is an adaptation that improves the chances of locating and successfully striking prey in low light (5). For example, the specialized hearing of barn owls, which have highly elongated duct lengths, even compared with other strigiforms, enables them to catch prey with high accuracy in complete darkness on the basis of acoustic cues alone (25, 26).

In contrast to its scarcity in extant birds, moderate elongation of the endosseous cochlear duct is common in our sample of nonavian theropods, occurring in all alvarezsaurids; the hypercarnivorous Tyrannosauridae, Dromaeosauridae, and Troodontidae; and the secondarily herbivorous Therizinosauria (Fig. 3). Theropods, therefore, evolved increased hearing ability more frequently than in modern birds, although Oviraptoridae and Ornithomimidae have shorter ducts (Fig. 3) and may have relied on other senses.

Previous hypotheses of alvarezsaurid ecology (15, 16, 27) noted a distinctive combination of ecomorphological traits in geologically younger taxa such as *Shuvuuia*. These traits include dental reduction and a slender mandible, combined with fossorial adaptations of its forelimbs, and have been used to support hypotheses of specialized predation on colonial insects (15, 16). Our study additionally indicates low-light vision and specialized auditory capabilities, traits that are widespread among mammals but rare in dinosaurs, including birds. Myrmecophagous mammals have previously been suggested as analogs for alvarezsaurids (15, 16). However, we note that nocturnality, excellent hearing, and digging forelimbs occur much more widely in mammals that span a broad range of ecologies. Moreover, dental or mandibular reduction in mammals may not be a functional analog of dental or mandibular reduction in birds and other dinosaurs; extant birds with proportionally small crania or mandibles, such as galliforms, can have wide-ranging diets, and birds that consume small vertebrates can subdue their prey without the use of teeth. We therefore suggest that

derived alvarezsaurids such as *Shuvuuia* could have consumed a wide range of nocturnal invertebrates and potentially small vertebrates, and that fossorially adapted forelimbs had versatile functions, allowing excavation of shallow-burrowing or crevice-inhabiting animals from the substrate or vegetation.

Combined visual and auditory specializations for nocturnality evolved independently in mammals, birds, and, as reported in this study, nonavian dinosaurs, providing an example of convergent sensory evolution in vertebrates. The sensory paleoecology of dinosaurs remains poorly understood in general. Nevertheless, our findings provide information on deep evolutionary divergences of activity patterns among nonavian theropods and strong evidence for nocturnal specialization through 95 million years of alvarezsaurid evolution. Many living animals are active at night, but nocturnal communities remain poorly studied both today (28) and in the past. Identifying specialized night foragers such as *Shuvuuia* highlights the occurrence of diel partitioning among predators in Mesozoic terrestrial ecosystems. It indicates that richly sampled paleoecosystems such as the Djadokhta Formation hosted previously unrecognized nocturnal and diurnal subcommunities, and expands our understanding of the structure of past ecosystems and of the ecological traits of theropod dinosaurs.

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SUPPLEMENTARY MATERIALS

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Data S1 to S12
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MDAR Reproducibility Checklist

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Revealing behavioral secrets in extinct species

Extinct species had complex behaviors, just like modern species, but fossils generally reveal little of these details. New approaches that allow for the study of structures that relate directly to behavior are greatly improving our understanding of the lifestyles of extinct animals (see the Perspective by Witmer). Hanson *et al.* looked at three-dimensional scans of archosauriform inner ears and found clear patterns relating these bones to complex movement, including flight. Choiniere *et al.* looked at inner ears and scleral eye rings and found a clear emergence of patterns relating to nocturnality in early theropod evolution. Together, these papers reveal behavioral complexity and evolutionary patterns in these groups.

Science, this issue p. 601, p. 610; see also p. 575

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