PALEONTOLOGY

The early origin of a birdlike inner ear and the evolution of dinosaurian movement and vocalization

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Reptiles, including birds, exhibit a range of behaviorally relevant adaptations that are reflected in changes to the structure of the inner ear. These adaptations include the capacity for flight and sensitivity to high-frequency sound. We used three-dimensional morphometric analyses of a large sample of extant and extinct reptiles to investigate inner ear correlates of locomotor ability and hearing acuity. Statistical analyses revealed three vestibular morphotypes, best explained by three locomotor categories—quadrupeds, bipeds and simple fliers (including bipedal nonavialan dinosaurs), and high-maneuverability fliers. Troodontids fall with *Archaeopteryx* among the extant low-maneuverability fliers. Analyses of cochlear shape revealed a single instance of elongation, on the stem of Archosauria. We suggest that this transformation coincided with the origin of both high-pitched juvenile location, alarm, and hatching-synchronization calls and adult responses to them.

Birds (Aves) are the most functionally diverse fliers (*1*) and, save for humans and cetaceans, perhaps the most sophisticated vocal communicators among vertebrates (*2*, *3*). The early history of the acquisition of these locomotor and vocal abilities is obscure. Attempts to reconstruct the history of avian flight have relied primarily on the musculoskeletal anatomy of the forelimb (*4*) and the presence of asymmetric feathers (*5*). Putatively lift-capable wings, necessary for aerial locomotion, first appeared in some form in the last common ancestor of either Pennaraptora or Paraves (*4*); however, their presence alone is insufficient to demonstrate the sophisticated control of three-dimensional (3D) locomotion required for birdlike flight. Attempts to reconstruct the origin of complex vocalization that rely strictly on the functional anatomy of the vocal apparatus are hindered by a lack of preservation; a well-preserved vocal apparatus has been recovered from a single extinct reptile—a member of crown Aves, whose ancestral vocal abilities were never in question (*6*).

There is another approach to investigating these transitions that does not require the preservation of the organs that produce the physical action in question. This approach involves examining the structure of the sensory organs that, together with the brain, monitor and mediate the action (*7*–*9*). In the cases of both flight and communication, the components of the inner ear are potentially useful to infer behavior with this method. The inner ear is a multipart sensory structure—situated deep within the skull and surrounded by the neurocranium (Fig. 1)—whose form and function are thought to be intimately linked to behavior (*7*, *10*). It comprises two mechanosensory organs: (i) the vestibular labyrinth, composed of the three semicircular canals, which detect angular movement and acceleration, and the utriculus and sacculus, which respond to linear motion and (ii) the cochlea, composed of the lagena or cochlear duct and the perilymphatic duct, which detects sound in the form of aerial vibrations transmitted (in crown reptiles) from the middle ear (Fig. 1 and figs. S1 to S6) (*10*, *11*). These organs can be understood as two evolutionary modules subject to independent selective pressures related to locomotion and hearing. A geometric morphometric test for modularity supports this assumption (*12*) (table S7). Thus, the form of the vestibular system (semicircular canals and associated structures) is often taken as indicative of locomotor ability and habits (*11*, *13*), and the form of the cochlea is taken as a proxy for hearing range and sensitivity (*7*).

Reptiles are enormously varied in their locomotor habits, ranging from limbless, aquatic, and quadrupedal lepidosaurs to aquatic, bipedal, and flying archosaurs (*1*, *7*, *11*). Acoustic behaviors can be difficult to detect (*14*), but lepidosaurs are generally limited in vocal use and complexity, whereas archosaurs as a whole produce a wide array of vocalizations, especially for intraspecies communication (*15*). These vocalizations become particularly complex in birds (*16*). Vocal communication in reptiles typically requires the ability to detect high-frequency far-field sounds (*7*). A growing body of research is identifying morphology-behavior correspondences in both extant and extinct reptiles (*11*, *13*) as well as correspondences between hearing sensitivity and cochlear geometry among extant reptiles (*7*). However, past research is limited in taxonomic and/or anatomical scope; no all-reptile (including birds) analyses have been conducted, and few if any fossil taxa have been included.

Reptile inner ear geometry, modularity, and allometry

We conducted a comprehensive geometric morphometric analysis of 38 landmarks [on the basis of conserved anatomy and on previously identified homologous landmarks in previous analyses (*7*, *11*, *17*, *18*)] (fig. S6). We placed the landmarks on 3D digital endocasts extracted from micro–computed tomography (micro-CT) scans of the inner ears of 124 reptilian taxa, including four non-archosaurian archosauromorphs and seven nonavialan dinosaurs. Data entirely new to this study (fig. S1) (*19*) include the complete virtual inner ears of the early-diverging archosauromorph *Prolacerta*; the near-crown archosauromorph *Euparkeria*; the pterosaur *Anhanguera*; the early-diverging sauropodomorph *Thecodontosaurus*; and a range of pennaraptoran dinosaurs including the alvarezsauroid *Shuvuuia*, the oviraptorosaur *Citipati*, the dromaeosaur *Velociraptor*, two troodontids, and the avialan *Hesperornis*. We also extracted six new endocasts from extant and recently extinct taxa (fig. S2). We chose not to use semilandmarks in recognition of the potential for spurious signal or noise to be introduced [(*20*) but see (*21*)]. We recognize, however, that many researchers do use semilandmarks, including researchers who recently performed a large-scale analysis of avian ears (*22*). To ensure that our results would be comparable, we performed analyses of only the taxa from that work and recovered a nearly identical distribution of ears in morphospace (figs. S30 to 33). In general, the inner ear complex is thought to be bilaterally symmetrical across Vertebrata (*10*), and this has recently been confirmed in archosaurs (*18*). We nonetheless verified symmetry in a phylogenetically broad subset of our sample (figs. S74 to S77). This subsample included an owl (*Tyto alba*), whose inner ears we found to be as symmetrical as those of other taxa, despite the well-known asymmetry in the outer and middle ears in Strigiformes (*23*).

Our morphological dataset enabled us to reconstruct ancestral inner ear architecture at key nodes from Reptilia to Neoaves (Figs. 1 to 5 and figs. S1 to S5 and S27 to S29). We mined behavioral data on locomotion, diet, and social behavior from a comprehensive set of sources (*12*) (table S2). This allowed us to infer the behavior of extinct taxa on the basis of their position in morphospace relative to known functional and behavioral clusters, corroborated by unweighted pair-group method with arithmetic mean (UPGMA) analyses (figs. S71 to S73). We tested these associations using phylogenetic analyses of variance (ANOVAs) (Tables 1 and 2; see also tables S4 and S5 for Goodall's *F*) and canonical variates and

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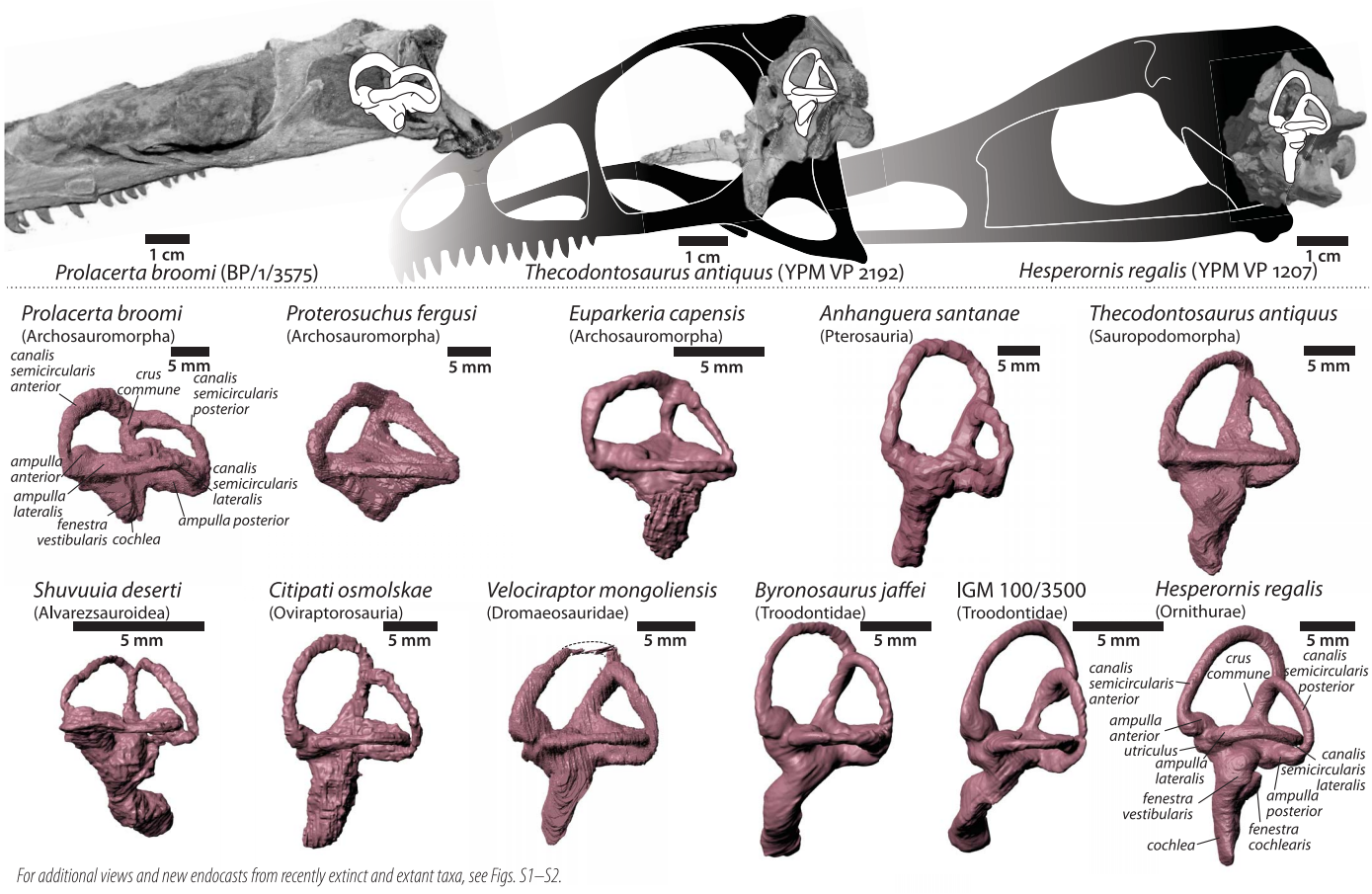

For additional views and new endocasts from recently extinct and extant taxa, see Figs. S1–S2.

Fig. 1. Selected archosauromorph inner ear endocasts. (**Top**) Cranial micro-CT scans and inner ear locations of selected fossil taxa new to this study. (**Bottom**) Inner ear endocasts of fossil taxa new to or newly segmented for this study. All images are original.

discriminant function analyses (figs. S60 to S70; for behavioral data and classifiers, see Figs. 2 and 3, figs. S7 to S26, and table S2) (*12*).

Although we analyzed whole-ear shape for our primary analyses, we also tested for and found significant modularity between the vestibular system and the cochlea (covariance ratio, 0.874; effect size, −3.384; $P = 0.002$ for the phylogenetic modularity test) (*12*). Therefore, we performed secondary and supplementary analyses on the vestibular and cochlear regions separately, using procrustes alignments derived from the whole-ear dataset and from the regional datasets alone (*12*) (tables S6, S7, S9, and S10 and figs. S7 to S10, S27 to S29, S34 to S39, and S44 to S51). We additionally analyzed the entire dataset to determine the effects of phylogeny, body size, and neurocranial anatomy on ear shape (vestibular, cochlear, and combined). As expected, whole ears, vestibular systems, and cochleae showed significant phylogenetic signal (table S6), both across all reptiles and within many more exclusive clades. To account for this signal, we conducted phylogenetic significance tests and analyses in addition to traditional nonphylogenetic analyses (*12*).

We tested for allometric scaling by plotting both centroid size and log-transformed body mass against whole-ear, semicircular canal, and cochlea shapes (*12*) (figs. S23 to S26; body-mass estimates were available for only a subset of fossil taxa). The results indicate a low correlation between size and shape [coefficient of determination (R^2) of 0.037 for centroid size versus whole ear and 0.22 for mass versus whole ear], which suggests weak allometric influence on ear anatomy. Clusters identified in the principal components analyses (PCAs) are broadly distinct and seem to be explained by locomotor and behavioral factors as discussed below. The functional signal we identify therefore appears to be largely independent of allometry: It is stronger than the allometric signal and it holds within as well as among the various clusters responsible for the appearance of allometric scaling. This stands in contrast to the conclusions of a recent study of bird semicircular canals (*22*), in which the allometric signal was found to be much stronger than the functional. The data analyzed in this study consisted of semicircular canal curvature and intercanal angle; the authors did not include the additional static vestibular landmarks that we used, but instead primarily relied on a large number of sliding semilandmarks along a midline curvature defined with static landmarks solely at the start and endpoints of the semicircular canals. Additional regions of the vestibular system (e.g., the ampullae or utricular regions) were not investigated, nor was the cochlea a subject of the study, because its focus was on locomotion. We suspect that a combination of broader phylogenetic scope and increased coverage of inner ear shape in our study, with static landmarks to better capture more homologous or partially homologous regions, contributes to these differences, in addition to our consideration of previously untested functional and behavioral variables using several statistical methods.

We considered the possibility that skull shape constrains ear shape to some extent, as has been suggested in some recent work (*22*). We argue instead that the relationship is likely one in which ear shape helps to determine the shape of the skull, especially the surrounding neurocranium. Embryonically, inner ears are formed long before skeletal tissues differentiate (*24*, *25*). They are placodal derivatives and their morphogenesis is substantially under

the control of a poorly understood set of intrinsic factors (*26*). The inner ears are, in turn, known to generate paracrine signals that affect skeletogenic mesenchyme (*26*, *27*), and it is clear that they also have substantial mechanical influence on the developing chondrocranium (*24*, *27*); indeed, much of the braincase develops as a sheath for the labyrinth (*28*). We hypothesized that skull shape would be correlated with ear shape owing to the ear's function as a morphogenetic signaling center. We focused on the posterior neurocranium, which is the part of the skull that develops in association with the inner ear. As predicted, phylogenetic two-block partial least-squares tests yielded modest correlations between skull shape and both vestibular and cochlear shapes; the vestibular effect size was considerably larger than the cochlear (*12*) (table S7 and figs. S44 to S51). Neurocranium-shape clusters are fewer and less well-separated than ear-shape clusters, which are best explained by locomotor and vocal function, as described below. This disparity is consistent with the idea that the ear is just one of multiple influences on the development of the skull. For example, it is known that other neurosensory structures, including the brain itself, play a role in patterning the skull (*29*, *30*).

Reconstructed ancestral inner ears

Reconstruction of ancestral inner ear shapes revealed that the inner ears of early-diverging archosauromorphs closely resemble those of lepidosaurs and turtles, and of the inferred ancestral reptile, in having anteroposteriorly broad vestibular systems and short cochleae (Fig. 5 and figs. S4 and S5) (*31*). Crown-clade archosaurs have taller and more acutely arched anterior semicircular canals, long cochleae, and reduced saccular and vestibular fenestrae (Figs. 2 to 5 and figs. S1 to S5). A tall anterior semicircular canal evolved early within Avemetatarsalia, a trend that continued further in late-diverging paravians (Figs. 1, 2, and 5 and fig. S4). Pterosaurs convergently developed a paravian-like condition, as has been observed previously in qualitative analyses [(*11*, *32*, *33*) and comments on pterosaur ear evolution in (*12*)]. For comments on several interesting features of individual inner ear endocasts, see the supplementary materials (*12*).

Vestibular system

Our analyses of the entire ear and of the isolated vestibular system (Figs. 2 and 3, Table 1, table S4, and figs. S19 to S22 and S60 to S67) (*12*) show overall division of extant taxa into three distinct, largely nonoverlapping vestibular morphology clusters, also appearing in UPGMA analysis (figs. S71 to S73). We examined the structure of the data by testing the explanatory power of a series of behavioral hypotheses (Table 1, table S4, and figs. S60 to S67). Phylogenetic ANOVAs revealed significant differences among taxa with different locomotor modes. Quadrupeds, limbless taxa, bipeds, and fliers all had significantly different vestibular shapes, with an especially strong signal for flying versus flightless taxa across the entire sample. There was also a strong signal for aquatic and semiaquatic habitats. Taxa that exhibit aerial predation, a behavior strongly associated with high-maneuverability or sophisticated flight, were significantly different from taxa that do not. Taxa in nonlocomotor behavioral and ecological categories, on the other hand, did not have significantly different vestibular shapes. Canonical variate and discriminant function analyses of whole-ear and vestibular-system geometries showed very strong predictive power for locomotor mode including flight (99.2 to 100% discrimination of confusion matrices; 86.4 to 98.4% discrimination of jackknifed confusion matrices), for

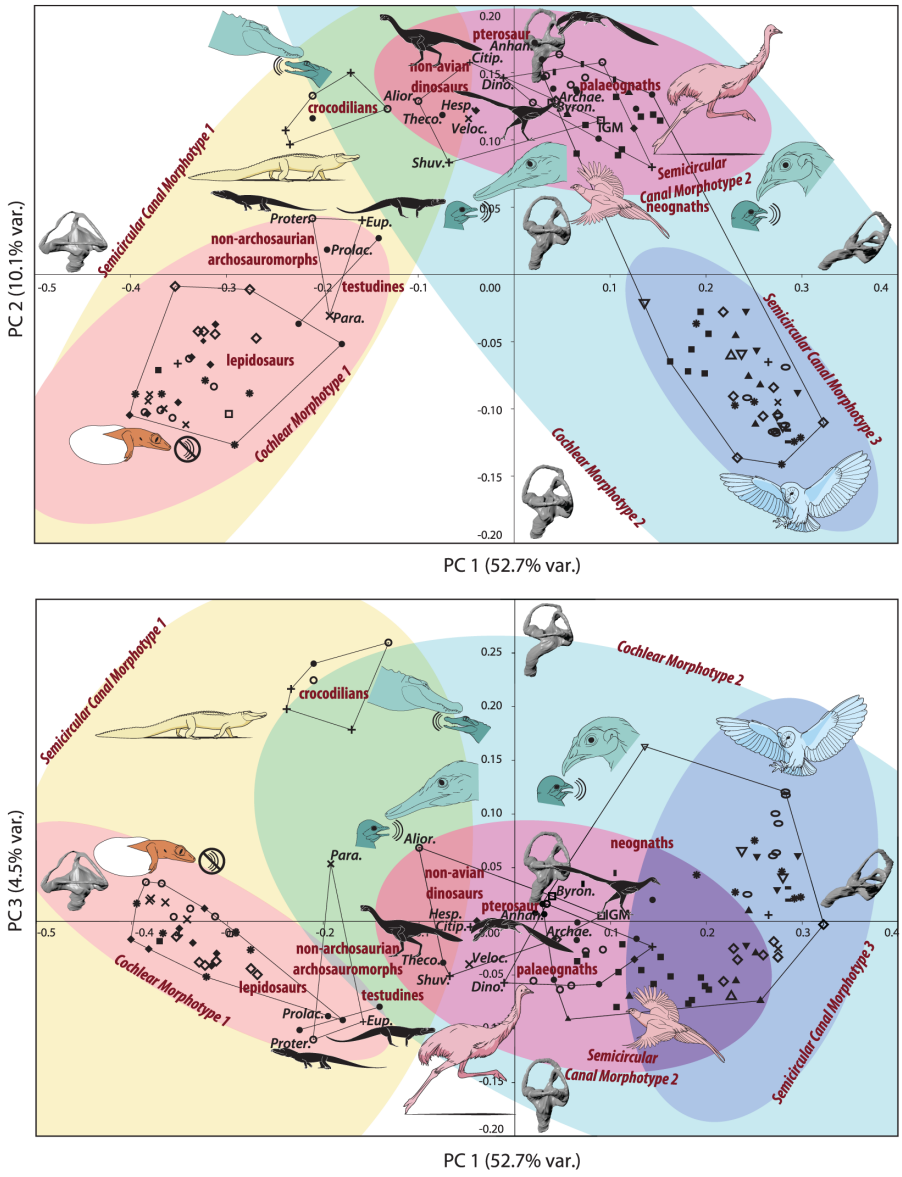

Fig. 2. PCA plots of reptilian inner ears and phylogenetic distribution of functional morphotypes. (**Top**) PCA of principal component 1 (PC1) to PC2. (**Bottom**) PCA of PC1 to PC3. Colored zones represent 99.7% confidence intervals based on behavioral data, and they also correspond to the three vestibular system morphotypes and two cochlear morphotypes discussed here [see Figs. 3 and 4 and (*12*)]. Abbreviations indicate the following taxa: Anhan., *Anhanguera santanae*; Archae., *Archaeopteryx lithographica*; Byron., *Byronosaurus jaffei*; Citip., *Citipati osmolskae*; Dino., *Dinornis robustus*; Eup., *Euparkeria capensis*; Hesp., *Hesperornis regalis*; IGM, unnamed troodontid IGM 100/3500; Para., *Parasuchus angustifrons*; Prolac., *Prolacerta broomi*; Proter., *Proterosuchus fergusi*; Shuv., *Shuvuuia deserti*; Theco., *Thecodontosaurus antiquus*; Veloc., *Velociraptor mongoliensis*. All images are original.

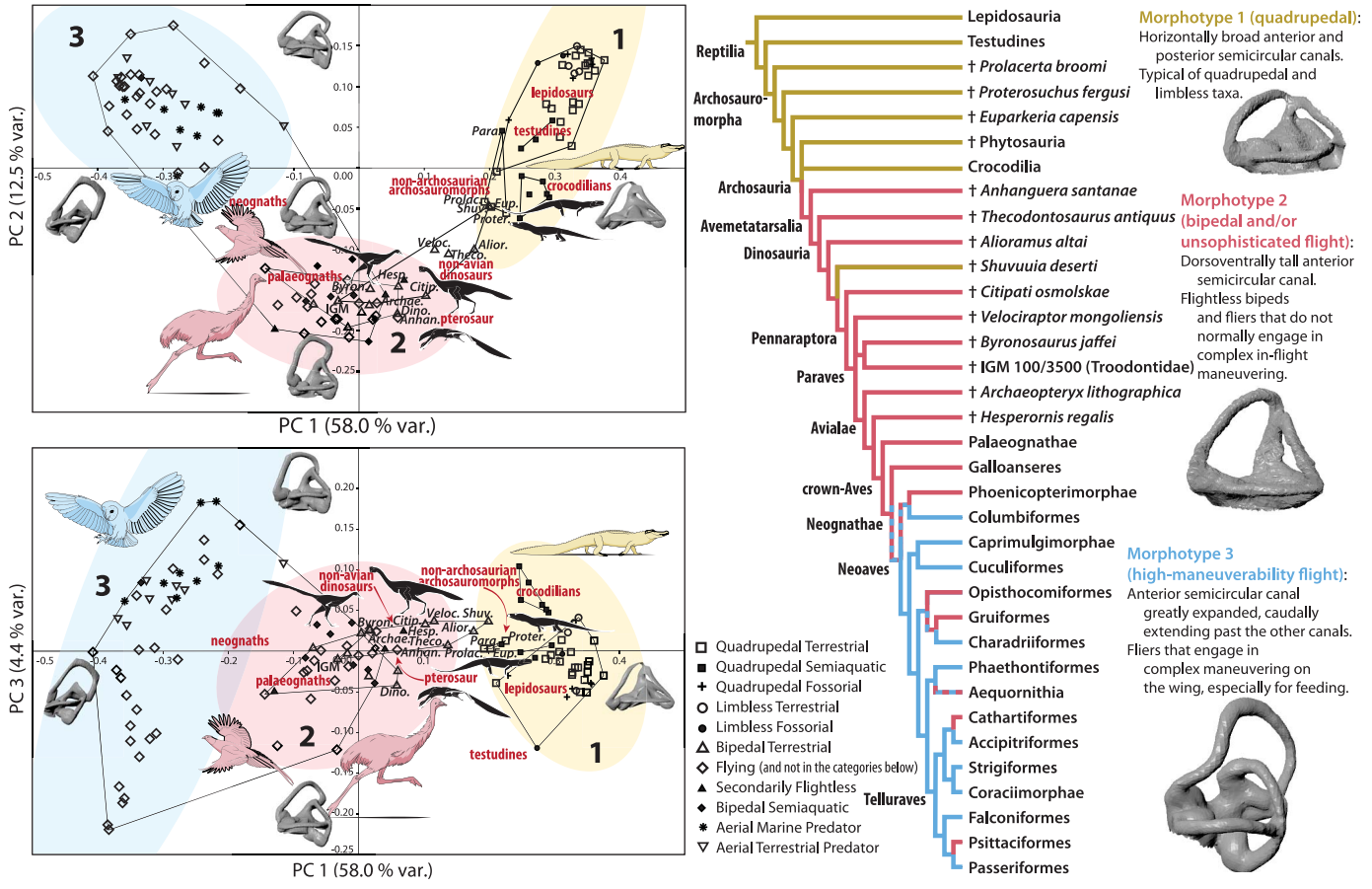

Fig. 3. PCA plots of reptile vestibular systems and phylogenetic distribution of functional morphotypes. (**Top left**) PCA of PC1 to PC2. (**Bottom left**) PCA of PC1 to PC3. Colored zones represent 99.7% confidence intervals based on behavioral data (*12*). (**Right**) Distribution of inner ear morphotypes (far right) on a tree of reptiles (right). Abbreviations are as in Fig. 2. All images are original.

aerial predation (97.6 to 99.2% and 81.3 to 84.6%), and for semiaquatic habits (99.2 and 83.2%) (figs. S60 to S67). Finally, we tested the correlation of whole-ear and vestibular shape with length ratios of forelimb elements, which have been used widely as proxies for locomotor style, particularly flight (*22*) (figs. S40 to S43). The strongest relationship (R^2 = 0.32) was with upper arm–to–lower arm ratio (humerus-to-radius), which is distinctively low in flighted taxa (*12*, *22*).

In sum, the three major PCA clusters in our analyses are best described as being distinguished by locomotor mode—one cluster comprising quadrupedal and limbless taxa (lepidosaurs and crocodilians); another comprising bipedal taxa, secondarily flightless taxa, and simple fliers; and a third consisting exclusively of taxa that engage in high-maneuverability flight behaviors, particularly related to feeding [for details of locomotor categories, see (*12*)]. This cluster of sophisticated fliers encompasses all aerial predators, including active raptorial species, aerial piscivores, and aerial insectivores. The ears of sophisticated fliers have a caudally enlarged anterior semicircular canal, where the majority of the canal is caudal to the *crus commune* and the canal often extends far caudal to the caudalmost extant of the posterior and lateral semicircular canals (Figs. 2, 3, and 5 and figs. S1 to S6 and S19 to S22).

All members of the high-maneuverability flight cluster are neoavian birds (Figs. 2 and 3 and figs. S19 to S22, S27 to S29, and S60 to S67), though some neoavian lineages have reverted to more characteristically non-neoavian flight behavior, and these cluster with flightless bipeds and less-sophisticated fliers along several axes. Reversals to an ancestral avian morphotype and behavior in Neoaves occur in a number of reluctant-flier lineages: grebes and flamingoes (Phoenicopterimorphae); loons and flightless penguins (early-diverging Aequornithes); the hoatzin (Opisthocomiformes); burst-adapted parrots (Psittaciformes); and, among raptorial bird clades, New World vultures (Cathartiformes), which are soaring scavengers that do not engage in aerial predation. The frequency of morphological reversals in disparate neoavian lineages with similar flight characteristics, along with statistically significant behavioral signals (Figs. 2 and 3, figs. S37 to S39 and S60 to S67, and table S4), demonstrates that neither phylogeny nor the shape of the surrounding skull or brain structures provides a complete explanation for the derived neoavian anterior semicircular canal. [In fact, the brains of flightless lineages, unlike the ears, are not predictably different from those of their flighted sister taxa (*8*, *34*).] Notably, morphological reversals also apparently occurred among some lineages of secondarily quadrupedal nonavian dinosaurs, which returned to the dorsoventrally short, rostrocaudally long vestibular system associated with quadrupedality (*31*, *35*, *36*).

Early-diverging archosauromorph taxa (*Prolacerta*, *Proterosuchus*, *Euparkeria*, and phytosaurs) fall, as expected, within the extant quadrupedal cluster (Figs. 2 and 3 and figs. S19 to S22) (*37*, *38*). Non-pennaraptoran dinosaurs plot in morphospace between extant quadrupeds and simple fliers. We consider this intermediate region to be indicative of nonflying bipedal locomotion, perhaps with a reasonable degree of 3D agility, turning, and

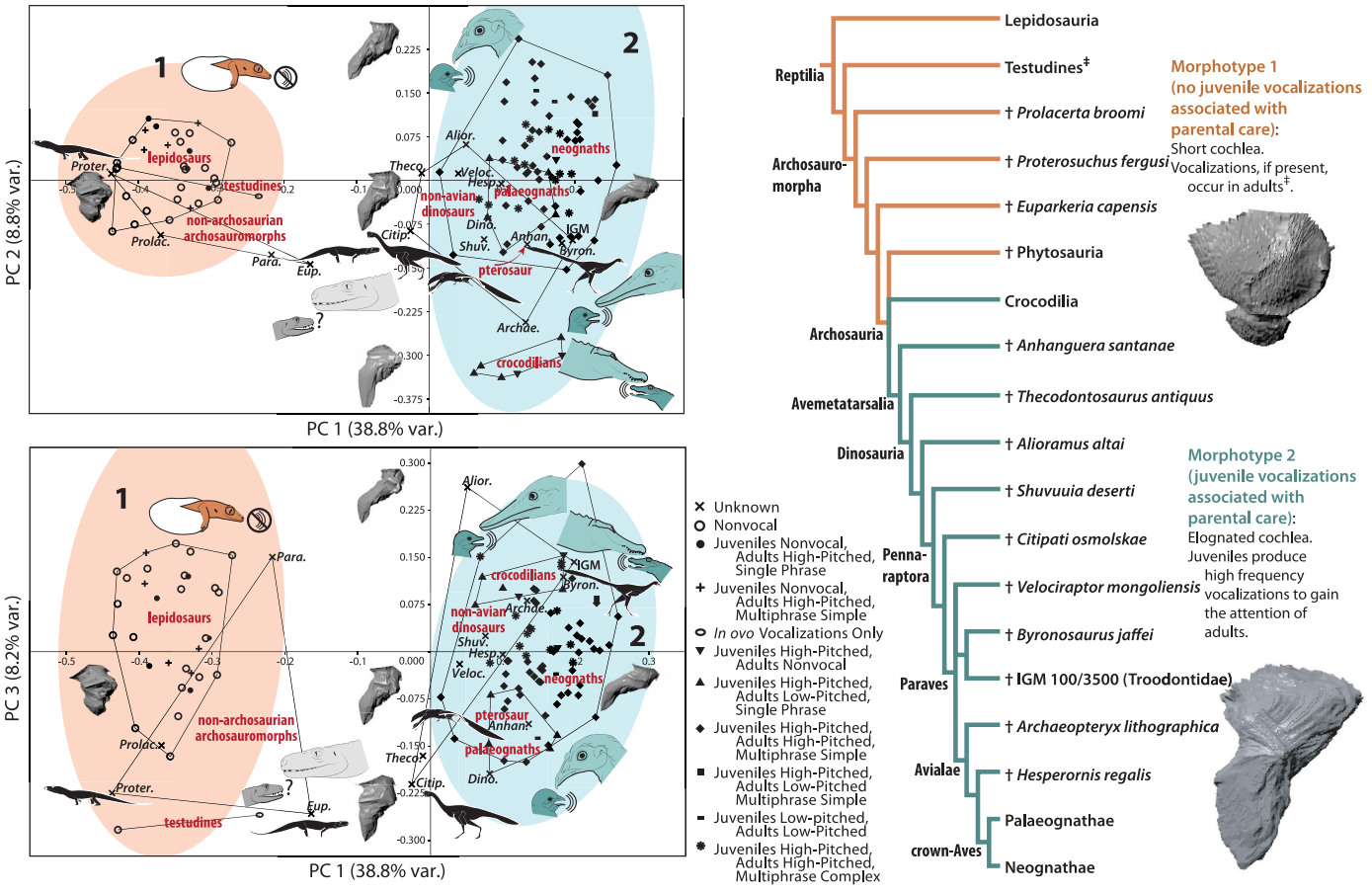

Fig. 4. PCA plots of reptile cochleae and phylogenetic distribution of functional morphotypes. (**Top left**) PCA of PC1 to PC2. (**Bottom left**) PCA of PC1 to PC3. Colored zones represent 99.7% confidence intervals based on behavioral data (*12*). (**Right**) Distribution of cochlea morphotypes (far right) on a tree of reptiles (right). Abbreviations are as in Fig. 2. All images are original.

acceleration—of the head, neck, or the entire body—and novel adaptations pertaining to the vestibulo-ocular and vestibulo-collic reflexes stabilizing the eyes and head during rapid and complex movements relative to the external environment (*8*). Notably, many small saurischian dinosaurs, aside from birds, had dexterous hands and feet and were of a size suited to climbing (*39*–*42*). *Citipati* and *Velociraptor*, representatives of early-diverging lineages within Pennaraptora—a clade distinguished by forelimbs bearing pennaceous feathers—fall just outside the simple-flier cluster (Figs. 2 and 3 and figs. S19 to S22 and S64 to S70) (*43*).

The whole-ear and vestibular-system morphologies of the pterosaur *Anhanguera* [(*11*) and comments on pterosaur inner ears in (*12*)], the Mesozoic avialans *Archaeopteryx* and *Hesperornis* (Fig. 1), and the troodontids *Byronosaurus* and IGM 100/3500 (an unnamed Cretaceous Mongolian troodontid) not only fall within the 99.7% confidence zone of bipedal taxa and simple fliers but also fall on the margin of (in the case of *Anhanguera*) or within the convex hull delineated by extant flying-bird species Figs. 2 and 3). However, discriminant function analyses identify them as flightless (figs. S60 to S63). In these pterosaurian, troodontid, and avialan taxa, the anterior semicircular canal is greatly enlarged dorsally compared with that of other avemetatarsalians and begins to extend caudal to the *crus commune* (Figs. 1 to 3 and 5 and figs. S1, S2, S5, and S19 to S22), a trend carried further in sophisticated fliers. This dorsal and caudal expansion may reflect greater specialization to locomotion in a highly 3D environment—an adaptation to either arboreality or early forms of volant activity. The notably birdlike morphology of the troodontid inner ear supports recent phylogenetic hypotheses that posit that at least some "troodontids" are not part of a clade that is sister to Dromaeosauridae as is the prevailing consensus (Deinonychosauria), but are rather part of a monophyletic or paraphyletic assemblage closer to Avialae (*44*).

The alvarezsauroid *Shuvuuia* (Figs. 2 and 3 and fig. S1) represents an exceptional reversal to the ancestral reptilian condition wherein the semicircular canals are approximately equal in dorsoventral height, and the vestibular system is rostrocaudally longer than dorsoventrally tall. The fossil specimen studied (IGM 100/977) is well preserved in three dimensions, and the braincase is uncrushed. *Shuvuuia* nests among taxa that otherwise have the dorsoventrally tall vestibular system that is typical of dinosaurs, and our ancestral shape reconstructions (Figs. 2, 3, and 5 and figs. S4, S5, and S19 to S22) indicate that the taller-than-long vestibular system is ancestral for saurischian dinosaurs. The condition seen in *Shuvuuia* is, therefore, best explained as a marked reversal among theropods, and it may be related to a suite of other adaptations to an insectivorous lifestyle (*45*–*47*). Despite being bipedal with long legs suitable for running, alvarezsauroids might have been more restricted to a more low-lying, if not fossorial, lifestyle than other theropods, owing either to the ground-dwelling habits of their eusocial insect prey or to an inability to climb with their highly modified forelimbs and comparatively uncurved pedal unguals (*48*). Outside crown birds (*49*–*51*), specialized

Table 1. Results of phylogenetic ANOVAS (1000 iterations) for behavioral signal in the semicircular canals. In the significance column, two asterisks indicate a very significant *P* value <0.01, a single asterisk indicates a significant *P* value <0.05, a period indicates a *P* value <0.1, and an empty cell indicates a *P* value >0.1. See also table S5 for additional analyses and table S2 for behavioral categories. R^2, coefficient of determination; *F*, Goodall's *F*.

Clade	R^2	*F*	*P* value	Significance
		Locomotion (all)		
Reptilia	0.02218	1.3837	0.095	.
		Locomotion (limbless versus quadrupedal)		
Lepidosauria	0.07072	2.2069	0.031	*
		Locomotion (bipedal versus quadrupedal plus limbless)		
Reptilia	0.00967	1.2006	0.227	
Archosauromorpha	0.01216	1.1078	0.261	
Archosauria	0.01127	0.98	0.361	
Avemetatarsalia	0.01446	1.174	0.225	
		Locomotion (all types): flight		
Reptilia	0.01594	2.0318	0.034	*
		Locomotion (bipedal-nonbipedal): flight		
Reptilia	0.01594	2.0218	0.035	*
Archosauromorpha	0.02002	1.8699	0.047	*
Archosauria	0.01481	1.3129	0.202	
		Locomotion (flying versus flightless)		
Reptilia	0.01985	2.4913	0.005	**
Archosauromorpha	0.02495	2.3034	0.022	*
Archosauria	0.02608	2.3032	0.028	*
Avemetatarsalia	0.02454	2.0126	0.032	*
		Locomotion (bipedal flying versus bipedal flightless)		
Dinosauria	0.02375	1.9223	0.041	*
Maniraptora	0.02433	1.92	0.044	*
Avialae	0.02379	1.7546	0.062	.
Aves	0.02387	1.7116	0.082	.
Palaeognathae	0.40336	3.3803	0.061	.
Neognathae	0.0171	1.096	0.336	
		Aerial predation (general presence or absence)		
Reptilia	0.05365	3.458	0.001	**
Archosauromorpha	0.06747	3.2195	0.001	**
Archosauria	0.06863	3.1316	0.001	**
Avemetatarsalia	0.06898	2.9264	0.001	**
Dinosauria	0.07139	2.9983	0.001	**
Maniraptora	0.07342	3.011	0.002	**
Avialae	0.07334	2.8096	0.001	**
Aves	0.06272	4.6841	0.001	**
Neognathae	0.06937	4.6958	0.001	**
Neoaves	0.07245	4.3741	0.001	**
		Semiaquatic lifestyle		
Reptilia	0.02794	3.536	0.001	**
Lepidosauria	0.01686	0.4974	0.867	
Archosauromorpha	0.04281	4.025	0.001	**
Archosauria	0.04606	4.1527	0.001	**
Avemetatarsalia	0.04892	4.115	0.001	**
Dinosauria	0.04964	4.1267	0.002	**
Maniraptora	0.05087	4.1273	0.003	**
Avialae	0.05612	4.2805	0.001	**
Aves	0.06021	4.4847	0.001	**
Neognathae	0.06822	4.6123	0.001	**
Neoaves	0.08806	5.4073	0.001	**
		Aerial predation (all types)		
Neoaves	0.11498	2.3385	0.003	**
		Aerial predation and habitat (absent versus terrestrial versus marine)		
Neoaves	0.09616	2.9257	0.003	**
		Terrestrial aerial predation prey (absent versus vertebrates versus insectivorous)		
Neoaves	0.04442	1.2785	0.192	
		Insectivory		
Neoaves	0.02912	1.6799	0.096	.
		Piscivory		
Neoaves	0.01362	0.7732	0.649	
		Active vertebrate predation		
Neoaves	0.00845	0.4771	0.936	

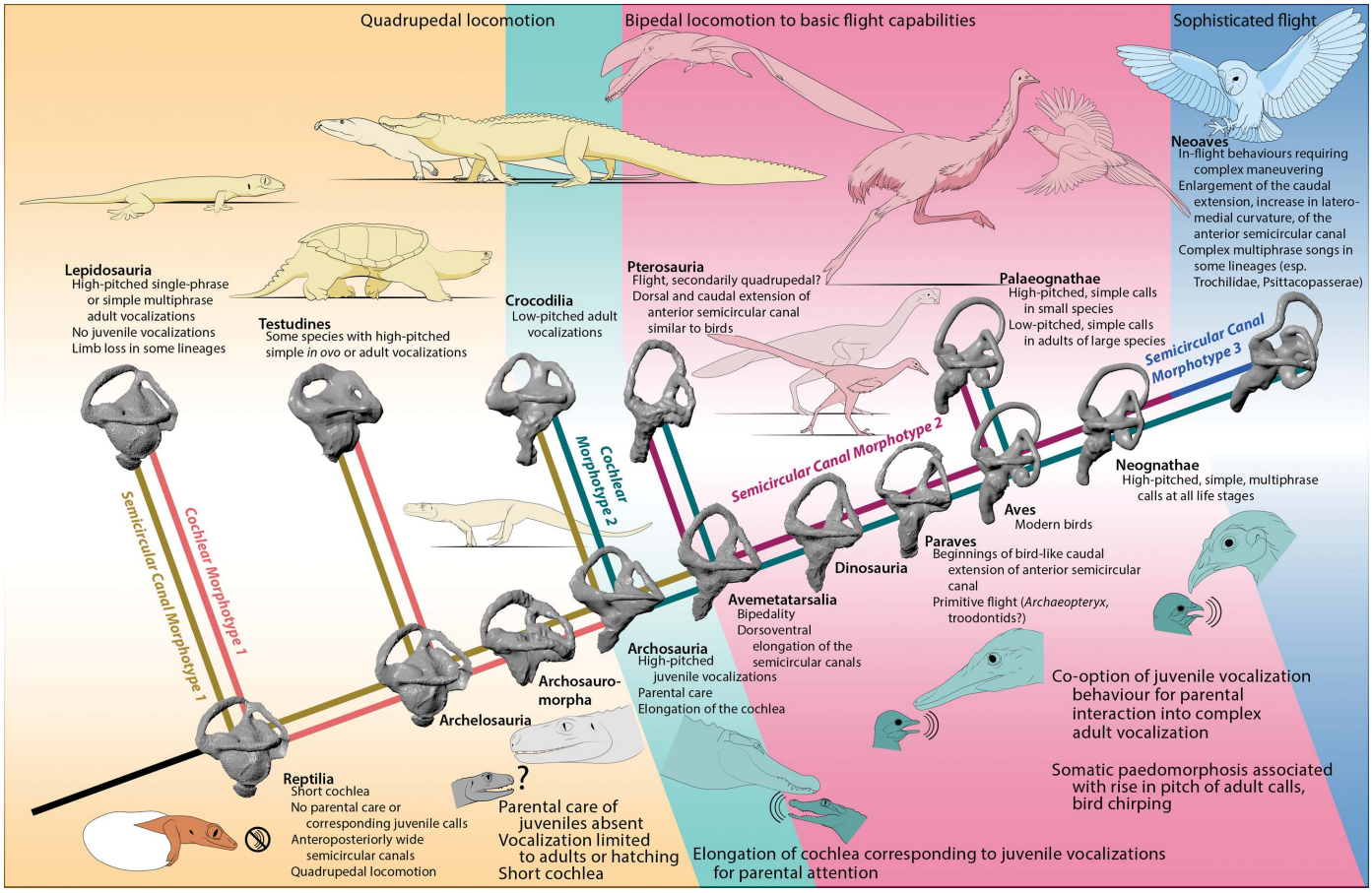

Fig. 5. Tree of reptiles showing changes in inner ear morphologies and inferred function. All images are original.

myrmecophagous tetrapod species within omnivorous, carnivorous, or otherwise non-eusocial insect–consuming clades also tend to have altered (often depressed) metabolic rates and modified movement coordination compared with their relatives (*52*, *53*).

Cochlear system

Extant reptile cochleae (Figs. 2 and 4 and figs. S19 to S22 and S68 to S73) fall into two distinct, nonoverlapping clusters identifiable in both the whole-ear and cochlea-only analyses—one consisting of taxa with short cochleae (i.e., lepidosaurs and turtles) and the other consisting exclusively of archosaurs, all of which have elongated cochleae. The positions of fossils indicate that cochlear elongation occurred only once in the evolutionary history of reptiles, among the more crownward archosauromorphs, with *Euparkeria* and the phytosaur *Parasuchus* being intermediate in morphology between early archosauromorphs and crown archosaurs. The cochleae of the troodontids and of *Shuvuuia* are exceptionally elongated with distal inflections, apparently convergent modifications that may be indicators of specialized sensation and behavior; however, these qualitatively distinctive characteristics do not have a strong effect on the overall shape analysis [fig. S1 and extended anatomical discussion in (*12*)].

Walsh *et al.* (*7*) have demonstrated that an increase in cochlear length is associated with greater hearing sensitivity, especially at high frequencies. To infer hearing sensitivity of the fossil taxa in our dataset, we interpolated their cochlear-length measurements into basicranial length–scaled and log-transformed plots of Walsh *et al.* (*7*). These results [see (*12*): interpolation into Walsh *et al.* 2009; figs. S52 to S57] indicate that most Mesozoic saurischian dinosaurs studied, and the small archosauromorph *Euparkeria*, likely had an optimal hearing frequency between 3500 and 5500 Hz and best mean hearing frequencies between 2250 and 3250 Hz, as compared with lower-pitched optimal frequencies between 1000 and 3000 Hz [comparable to extant lepidosaurs and crocodilians (*10*)] in early-diverging archosauromorphs. Optimal hearing frequencies between 3500 and 5500 Hz are in the range of extant neognathous birds (*7*). The large theropod dinosaur *Alioramus* was convergent on early archosauromorphs in having a lower-pitch optimal frequency range.

Various explanations have been proposed for the evolution of increased hearing sensitivity in vertebrates, among them prey localization (*16*), predator avoidance (*54*), and intraspecies communication (*15*). As with the vestibular system, we tested for significant differences in whole-ear and cochlear shape associated with a range of behavioral characters using phylogenetic ANOVAs (Table 2 and table S5). Dietary characteristics failed to show a significant signal. This is in keeping with the fact that there is no indication that a change in prey type or size occurred at the same time as the cochlear elongation event in archosauromorphs, as both stemward and crownward taxa are inferred to have been generalized predators on small vertebrates (*55*). We did not test for a correlation between cochlear length and predation pressure because this pressure is difficult to score effectively for extant taxa and is effectively impossible to estimate for extinct taxa, but we see little reason that early archosauromorphs, beginning with *Euparkeria*, should have faced greater predation risk than their predecessors or than contemporary lepidosauromorphs. We did find a weakly significant signal for nocturnality within Reptilia

Table 2. Results of phylogenetic ANOVAS (1000 iterations) for behavioral signal in the cochleae. As in Table 1, two asterisks indicate a very significant *P* value <0.01, a single asterisk indicates a significant *P* value <0.05, and an empty cell indicates a *P* value >0.1. See also table S6 for additional analyses and table S2 for vocalization quality categories.

Clade	R^2	*F*	*P* value	Significance
		Parental care		
Reptilia	0.0186	2.0473	0.042	*
Archosauria	0.01799	1.3737	0.179	
Aves	0.01924	1.3535	0.166	
Palaeognathae	0.23171	1.2064	0.4005	
Neognathae	0.01498	0.9582	0.341	
Neoaves	0.01448	0.8225	0.418	
		Nocturnal-diurnal		
Reptilia	0.01904	2.0965	0.012	*
Lepidosauria	0.10674	3.4653	0.002	**
Archosauria	0.01811	1.383	0.153	
Aves	0.01381	0.9665	0.444	
Palaeognathae	0.23171	1.2064	0.4025	
Neognathae	0.01621	1.0379	0.401	
Neoaves	0.01748	0.9963	0.431	
		Adult vocalizations, presence or absence		
Reptilia	0.00869	0.947	0.509	
Lepidosauria	0.03867	1.1667	0.268	
Archosauria	0.00656	0.4955	0.912	
Aves	0.00775	0.5387	0.846	
Neognathae	0.00825	0.5239	0.854	
Neoaves	0.00883	0.4987	0.848	
		Adult vocalizations, pitch		
Reptilia	0.01826	0.9953	0.475	
Lepidosauria	0.03867	1.1667	0.268	
Archosauria	0.01839	0.6934	0.84	
Aves	0.02259	0.786	0.686	
Palaeognathae	0.1832	0.8971	0.6165	
Neognathae	0.02727	0.869	0.524	
Neoaves	0.02915	0.8257	0.591	
		Adult vocalizations, complexity		
Reptilia	0.02537	0.9198	0.601	
Lepidosauria	0.05874	0.8736	0.629	
Archosauria	0.03987	1.0105	0.424	
Aves	0.04314	1.007	0.412	
Palaeognathae	0.21798	1.1149	0.3115	
Neognathae	0.0336	1.0777	0.336	
Neoaves	0.03437	0.9789	0.387	
		Juvenile vocalizations (all high-frequency), presence or absence		
Reptilia	0.03483	3.8969	0.001	**

and a strongly significant signal within Lepidosauria, which may relate to the differing sensory demands of nighttime activity. However, there was no significant activity-pattern signal in other clades. With regard to communication, presence, pitch, and complexity of adult vocalization did not show significant signal. However, the presence of high-pitched juvenile vocalization showed a strong signal (P = 0.001), and parental care also showed some signal for all reptiles (P = 0.042). Canonical variate and discriminant function analyses on cochlear geometry showed very strong predictive power for juvenile vocalization (99.2% discrimination of confusion matrices; 92.0% discrimination of jackknifed confusion matrices) and parental care (97.6 and 85.6%, respectively) (figs. S68 to S70).

The major vocal behavior differentiating archosaurs from other reptiles is the use of juvenile calls or chirps to gain the attention of, and provide spatial information to, parents or other adult caregivers (*56*, *57*). Unlike adult vocalizations, juvenile vocalizations are universally high pitched (*7*). The association of juvenile calls with parental care is borne out by statistically significant cochlear signal for both behavioral phenomena. It should be noted that the evolution of altriciality is distinct from the evolution of juvenile vocalization and parental care. According to our ancestral state reconstructions (fig. S59), ancestral archosaurs had precocial young; altriciality is restricted to some neoavian clades (*58*). Notably, many archosaurian juvenile calls are location calls (*7*), which are primarily useful for precocial offspring capable of traveling independently.

We note that an instance of cochlear elongation in mammals, on the stem of Theria, is also associated with the evolution of juvenile vocalization. Monotremes have a long but uncoiled cochlea, which appears to be the ancestral condition for Mammalia, if not Mammaliaformes (*59*). Therian mammals further elongate their cochleae into coiled

structures (*59*). Both monotremes and therians vocalize as adults; however, as juveniles, monotremes are not known to vocalize (*60*–*63*). It is in therians that high-pitched juvenile chirps to gain and maintain the attention of adults first occur (*62*), along with the therian coiled cochlea (*59*).

As the correlation of elongated cochleae with high-pitched juvenile calls seems to relate to parental care, the presence of intermediately elongated cochleae in some later-diverging archosauromorphs, such as *Euparkeria* and perhaps phytosaurs, indicates that archosaurian parental care and associated vocal behavior may have originated outside crown-group archosaurs in these later-diverging archosauromorphs (Fig. 4). Ancestral archosaurs can be inferred to have had low-pitched, closed-mouth adult vocalizations like those of modern crocodilians and some large flightless birds (*64*) [see also (*12*) and table S2]. As in modern crocodilians and non-neoavian birds, the precocial offspring of these ancestral archosaurs may have used a set of high-pitched calls to gain the attention of adults (*56*, *57*). The complex high- and low-frequency vocalizations of adult archosaurs, and adult sensitivity to wide ranges of sound frequencies not typically produced by other conspecific adults (*7*), may be a subsequent evolutionary novelty enabled by the greater hearing sensitivity brought about by cochlear elongation, which evolved in tandem with parental behaviors. Autapomorphic low-frequency hearing in *Alioramus* could reflect anomalously low-pitched juvenile calls or possibly a derived lack of parental care as seen in megapodiid and apterygid birds (*49*, *50*, *51*, *58*). Although we found little cochlear signal for diet, it is also possible that low-frequency optimal hearing assisted in the detection of sounds made by large prey [(*65*) but see (*66*)].

Discussion

Our analyses demonstrate that inner ear variation is structured in predictable ways across large evolutionary distances, and that this variation is correlated with locomotor behavior and hearing acuity in those taxa for which such data are available. The markedly avian semicircular canals of troodontids (Figs. 2 and 3 and fig. S1) suggest that these dinosaurs had locomotor control comparable to that of pterosaurs, *Archaeopteryx*, and early-diverging crown birds (Figs. 1 to 3 and 5). Many neoavian birds have a modified semicircular canal structure associated with high-maneuverability flight, aerial feeding, and predation that suggests these behaviors originated in this clade, but this group also exhibits reversals in vestibular-system structure corresponding to derived losses of these behaviors. The elongated cochleae of archosaurs and relatives such as *Euparkeria* suggest that certain complex social behaviors such as parental care may have originated as early as the Triassic and before crocodilians diverged from birds (Figs. 2, 4, and 5). Juvenile vocalizations may have been an innovation that brought about greater aural sensitivity in adult archosaurs, permitting them to respond to a wider repertoire of social calls than observed in other reptiles (*15*). High-pitched calling in adult birds may even be a paedomorphic retention of juvenile dinosaurian vocal capabilities.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/372/6542/601/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S77
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MDAR Reproducibility Checklist

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The early origin of a birdlike inner ear and the evolution of dinosaurian movement and vocalization

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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 archosauromorph 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.

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