

ending in the fenestra pseudorotunda? The next trunk could then represent nerves X and XI and the third trunk nerve XII. The point here is that Whetstone and Martin's interpretation of a complex morphological structure from casts is questionable, and alternative explanations are possible.

Notwithstanding these questions of interpretation, which simply reflect the shortcomings of attempts to reconstruct the soft anatomy of fossil organisms, it is interesting that other workers have reported a fenestra pseudorotunda in the theropods *Dromaeosaurus*⁴ and *Gallimimus*⁵, and in the pachycephalosaurians *Prenocephale* and *Homalocephale*⁶. In *Dromaeosaurus*⁴ remnants of the stapes confirm the interpretation of the fenestra ovalis, and the adjacent aperture, identified as the fenestra (pseudo) rotunda (though identified as the IX foramen by Whetstone and Martin), bears a relationship with the fenestra ovalis which is strikingly similar to that illustrated by Whetstone and Martin for *Hesperornis* and *Alligator* (compare ref. 4, Fig. 7a, and ref. 1, Figs. 3a,b).

Whetstone and Martin marshalled evidence from embryology to support their case that the 'round window' (fenestra pseudorotunda) of birds and crocodiles is a homologous feature unique to them. Although other living vertebrates (mammals and lizards) also have round windows, they argued that the structure had a similar embryology in birds and crocodiles, and that this differed from that of other vertebrates. However, if some dinosaurs do indeed have a fenestra pseudorotunda, then the embryological evidence in support of its homology in birds and crocodiles is less compelling. The similar embryology of the otic regions of crocodiles and birds may only reflect their archosaurian ancestry.

The other character described by Whetstone and Martin, periotic sinuses associated with bones of the middle ear cavity, also may not be unique to crocodiles and birds. Depressions have been described in the lateral wall of the braincase of *Saurornithoides*⁷ that seem to be associated with the middle ear.

Thus, we find that the evidence presented by Whetstone and Martin to support an hypothesis of common ancestry of crocodiles and birds independent of dinosaurs is equivocal. It is sobering to recount Baird's⁸ summary statement in 1970: 'Parallelism and convergence in the tympanic regions of living reptiles are common, and only a few reptilian ears are yet known in detail.' Thus, even if Whetstone and Martin are correct in their assertion that a fenestra pseudorotunda and periotic sinuses are unique to birds and crocodiles, it remains to be determined whether this is due to common ancestry or convergence. In view of the extensive evidence compiled by Ostrom⁹⁻¹⁴ for common ancestry of birds

and dinosaurs, the otic features mentioned by Whetstone and Martin may best be ascribed to homoplasy.

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WHETSTONE AND MARTIN REPLY—The fundamental difference between the otic capsules of *Sphenodon* and those of a bird or crocodile is in the course of the perilymphatic duct. In *Sphenodon*, it turns medially, enters the endocranium and passes along a groove before being exposed to pharyngeal tissues¹. In birds and crocodiles, it turns laterally and is exposed to the tympanic cavity. Either condition requires a correlated suite of osteological structures. We have used these structures in attempting to determine the course of the duct in dinosaurs². Hadrosaurs and *Ankylosaurus*, for example, are like *Sphenodon* but unlike birds or crocodiles, in having an open 'vestibule' to the endocranium, a groove between the vestibule and vagus foramen, and no confluence between the external cranial openings. Whether or not the duct left the cranium alone (as suggested by McGowan and Baker) is irrelevant to the problem at hand. Either interpretation presumes a primitive (medial) course for the duct, along the braincase wall.

By using a bird or crocodile as a model for fossil archosaurs, some workers have

restores a fenestra pseudorotunda in dinosaurs. The foramen identified³ as the 'round window' in *Gallimimus* is not on the otic capsule, but is far up on the parocciput. In the type of *Dromaeosaurus*, the right otic capsule has been destroyed, along with the footplate of the stapes. The resulting hole and the remnants of a nerve canal were labelled 'Foramen Rotundum' in the original restoration⁴. The ear regions of the cited pachycephalosaurs are indeterminate. The best candidate for the presence of this structure is the ornithischian, *Hypsilophodon*. Were a 'window' present in dinosaurs, it would not lessen the embryological evidence for the homology of the fenestra in birds and crocodiles, but might indicate that the homology evolved in a more remote ancestor.

Ostrom's evidence for a theropod origin for birds has been well summarized⁵. The evidence for a 'sister-group' relationship to crocodylians, first suggested by Walker⁶, is still being developed by Whetstone, but the following derived features seem to be homologous: a fenestra pseudorotunda; a pneumatic quadrate; a foramen aereum in the lower jaw; periotic pneumatic cavities in the dorsal, central and rostral positions; a quadrate cotylus at the anterior base of the parocciput; a bipartite quadrate articulation with dermal and endochondral bones—anteriorly with the prootic, squamosal and laterosphenoid, posteriorly with the prootic and otocipital; a squamosal shelf over the ear region; antero-medial origin of the temporal musculature; two pneumatic cavities surrounding the cerebral carotid; unserrated teeth with a constricted neck⁷; bony tooth roots with an enclosed, oval resorption pit⁷. None of these features is known in theropod dinosaurs. The 'lateral depression' of *Saurornithoides* has no similarity to the periotic sinuses.

On the basis of present evidence, we feel that an argument of close relationship to crocodylians is the most parsimonious hypothesis available for the ancestry of birds.

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