

MATTERS ARISING

Pyroclastic sulphur

FRANCIS *ET AL.*¹ recently commented on the apparent rarity of pyroclastic sulphur in terrestrial eruptions. They described sulphur-rich ejecta from Poás volcano, Costa Rica, and mentioned the presence of myriads of small, sulphur spheres. Similar spheres have been reported in tephra erupted from Ruapehu²⁻⁴, New Zealand, and may well be common at many volcanoes where an active vent is occupied by a crater lake.

The Ruapehu spheres range from 50 μm to 1 mm, but most are 125–750 μm in diameter. They have a lustrous, granular surface, and comprise solid, black, orthorhombic sulphur with disseminated silicate, and iron sulphide dust, a few small vacuoles and rare, yellow sulphur crystals. Some are globular, some are fused double-spheres, but most are almost perfectly round 'rough' spheres'. They were ejected in abundance by phreatomagmatic eruptions in 1971, and one fine ash collected 15 km downwind comprised 12% by volume of spheres². Sulphur also occurs in Ruapehu tephra as uncommon, angular, yellow fragments, and sulphur drip on ejected blocks. Rafts of spongy sulphur float on the lake in quiet or eruptive periods.

Vent morphology and activity of Ruapehu⁶ and Poás appear similar, and a subaqueous liquid sulphur lake has been postulated for both volcanoes^{7,8}. I agree with Francis *et al.*¹ that this is unlikely. Much consolidated, volcanoclastic/chemogenic sediment has been erupted from Ruapehu, and in some siltstones ejected in 1971, sulphur occurs as globules in cavities, and veins crossing the bedding. This I believe is evidence that sulphur is 'sweated' out of sulphurous sediment, whence it may enter superheated steam fumaroles and be discharged violently into muddy lake water to form black droplets. The lack of coarse, clastic or scoriaceous sulphur suggests that there were no large accumulations of liquid sulphur present when the lake bed was fragmented during phreatomagmatic eruptions of Ruapehu.

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FRANCIS REPLIES—We were not aware of the existence of small sulphur spherules in the material ejected by the Ruapehu eruption of 1971, and are grateful to Wood for bringing it to our attention. We agree that such spheres may well be common in active volcanoes with crater lakes, and would welcome any further observations of these and related phenomena.

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Recombination intermediates

IN the summary of their elegant demonstration of adenovirus recombination intermediates, Wolgemuth and Hsu¹ state: "To the best of our knowledge, this is the first visualization of *in vivo* recombination intermediates of discrete DNA molecules isolated from eukaryotic cells". They appear to have overlooked the paper published last year by Bell and Byers² which presented an equally clear demonstration of Holliday-type recombination intermediates involving the 2- μm plasmids of *Saccharomyces cerevisiae*. Although this earlier case might be held to be atypical of recombination in general, in that it involved inverted repeats within the same molecule rather than homologous regions of different molecules, it was, in another respect, more relevant to meiotic recombination, because the Holliday structures were found specifically in cells at the prophase stage of meiosis.

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WOLGEMUTH AND HSU REPLY—As stated in the text of our paper, our study does indeed represent the first example, to the best of our knowledge, of visualization of *in vivo* recombination intermediates in animal cells and we are sorry that the word eukaryotic in the summary was misleading. We would like to emphasize

Fincham's point that our observations are more typical of recombination in that they are inter- rather than intramolecular. Our failure to cite the paper by Beck and Byers in our discussion was totally inadvertent and we had contacted them previously in this regard.

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Common ancestry for birds and crocodiles?

A PSEUDOSUCHIAN origin for birds and crocodiles, independent of dinosaurs, has been proposed by Whetstone and Martin¹. They described two 'derived' characters of the otic region of the skull, a fenestra pseudorotunda and periotic sinuses, which were claimed to be unique to crocodiles and birds and thus evidence for their common ancestry. It is well known that crocodiles and birds possess a similar otic morphology^{2,3}. Any hypothesis of their common ancestry independent of dinosaurs therefore depends critically on the assertion that dinosaurs do not have similar shared features, or that if they do, the features are not homologous. In this respect, we think that Whetstone and Martin's evidence is equivocal and should be treated with caution.

Whetstone and Martin note that in primitive reptiles the perilymphatic duct exits from the cranium through the vagus foramen (fissura metotica), accompanied by certain cranial nerves. In crocodiles and birds, however, the perilymphatic duct has a separate exit, and terminates in a small membrane that closes the fenestra rotunda, or, more correctly, the fenestra pseudorotunda². The fenestra pseudorotunda lies very close to the fenestra ovalis.

Based on their interpretations of casts of the inner ear structure, Whetstone and Martin concluded that dinosaurs did not have a fenestra pseudorotunda. Casts of four of the seven genera studied were illustrated: the sauropod *Brachiosaurus*, the hadrosaur *Lophorothon*, the ankylosaur *Ankylosaurus* and the theropod *Allosaurus* (see ref. 1, Fig. 2 a–d, respectively). We question how the authors can be certain that the single trunk identified in *Lophorothon* and *Ankylosaurus* does in fact represent both the perilymphatic duct and certain cranial nerves. Why should it not represent the perilymphatic duct alone? In *Lophorothon*, for example, could not the first trunk (labelled perilymphatic duct plus nerves X–XI) represent the perilymphatic duct exiting alone, and

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 arosom 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 otocapital; 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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