

and they may well be prints of the same (left) foot. Both prints seem to show the same pattern of asymmetry—weak outward curvature of digit 3, and an angle of divarication between digits 2 and 3 which is slightly greater than that between digits 3 and 4. Mid-way between these two footprints is a poorly defined surface feature which was regarded by Brown⁶ as an amalgam of two footprints from other dinosaur tracks. This feature is probably an incomplete print of the ornithopod's right foot; it is about the same width as the other two footprints and shows traces of three digits with an appropriate pattern of divarication. The three footprints have a pattern of digit spacing (digit 2 slightly more divergent than digit 4) which is characteristic of many ornithopod footprints⁵ and which is consistent with their identification as left, right and left. This interpretation also reveals distinct positive (medial) rotation of the footprints, an arrangement which is common in the trackways of other bipedal dinosaurs (see, for example, refs 8 and 9); no such footprint rotation is evident in Brown's interpretation.

According to the revised interpretation (Fig. 1b) Brown's measurement of 15 feet would actually represent a stride (between successive prints of the same foot). Using Alexander's method¹, it may then be calculated that the Colorado ornithopod was walking (with λ/h of 1.34) at a speed of 2.4 m s^{-1} (8.5 km h^{-1}). The highest speeds so far estimated from dinosaur tracks are in the region of $3.6\text{--}4.3 \text{ m s}^{-1}$ ($13.0\text{--}15.5 \text{ km h}^{-1}$), and these are attributed to small bipedal runners with $h < 1 \text{ m}$ (refs 1,5). There are no reports of tracks indicating that larger bipedal dinosaurs were capable of achieving a running gait (with $\lambda/h > 2.0$).

I thank Dr E. S. Gaffney (American Museum of Natural History) for providing a description and illustrations of the Colorado footprints.

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RUSSELL REPLIES—Brown clearly uses 'stride' in the sense of step in his description¹: "The tracks... (show) the right and left foot in normal stride where the giant

had stepped 15 feet". He also describes a third footprint, made when the animal had stepped on a firmer substrate. The steps defined by the three footprints would presumably have been of comparable length or Brown would not have referred them to the same trackway. In view of the symmetry of hadrosaur footprints² and Brown's presence at the site where the trackway was excavated, prudence suggests that his interpretation remains as plausible as Thulborn's proposed alternative.

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Inhibition of haemoglobin S gelation and water structural effects

BENESCH AND BENESCH¹ recently proposed an interesting hypothesis concerning the mechanism of action of various hydrophobic molecules which inhibit the gelation of sickle cell haemoglobin (HbS). They suggested that this hydrophobic class of sickling inhibitors may act on water structure rather than interact directly with HbS. The physical explanation provided by Benesch and Benesch¹ for the 'melting' of the HbS gel at low temperatures seems very plausible. They suggest that the creation of more polyhedral void spaces in water at lower temperatures and the consequent coalescence of 'filled' (with nonpolar moieties) and 'empty' polyhedral cages is responsible for weakening the hydrophobic forces. However, they extend this reasoning to suggest that the inhibition of polymerization of HbS by a variety of compounds containing hydrophobic residues is also "brought about by competition between the water polyhedra filled with small hydrophobic molecules and those attached to the protein, rather than a direct interaction between the hydrophobic residues and the protein which should be stereospecific"¹. The two situations are not physically analogous.

The clumping of 'empty' and 'filled' polyhedral cages leads to the relief of hydrophobic interactions while the clumping of filled cages with other filled cages produces hydrophobic interactions². This will apply equally whether the cages are filled with nonpolar segments from the protein or the small hy-

drophobic molecules. When the latter are added to a solution containing the HbS polymer, some existing water polyhedral void spaces will be further occupied and the resulting encounter of cages filled with small hydrophobic molecules with those filled with nonpolar side chains of the protein should provide the stimulus for a direct (hydrophobic) interaction of the small molecule with the haemoglobin nonpolar side chains, in competition with the side chain–side chain interaction. Gel melting can occur, in such cases, by a substitution of protein–protein hydrophobic interaction with protein–small molecule hydrophobic interaction. This interaction may be weak or strong, depending on the nature of the molecule and the side chain. If, in addition to this hydrophobic interaction, ionic or hydrogen bonding is possible, the direct interaction will be further strengthened. Such a possibility has been postulated for a molecule like benzyl alcohol³, although there has been no direct proof of this.

The attempts to increase the effectiveness of hydrophobic antisickling agents by structural modifications have failed so far, not because the agents are incapable of direct interaction with the protein but because of stronger macromolecule–macromolecule interactions in the polymer.

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