The avian nature of the brain and inner ear of *Archaeopteryx*

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***Archaeopteryx*, the earliest known flying bird (avialan) from the Late Jurassic period, exhibits many shared primitive characters with more basal coelurosaurian dinosaurs (the clade including all theropods more bird-like than *Allosaurus*)[1], such as teeth, a long bony tail and pinnate feathers[2]. However, *Archaeopteryx* possessed asymmetrical flight feathers on its wings and tail, together with a wing feather arrangement shared with modern birds. This suggests some degree of powered flight capability[3] but, until now, little was understood about the extent to which its brain and special senses were adapted for flight. We investigated this problem by computed tomography scanning and three-dimensional reconstruction of the braincase of the London specimen of *Archaeopteryx*. Here we show the reconstruction of the braincase from which we derived endocasts of the brain and inner ear. These suggest that *Archaeopteryx* closely resembled modern birds in the dominance of the sense of vision and in the possession of expanded auditory and spatial sensory perception in the ear. We conclude that *Archaeopteryx* had acquired the derived neurological and structural adaptations necessary for flight. An enlarged forebrain suggests that it had also developed enhanced somatosensory integration with these special senses demanded by a lifestyle involving flying ability[4].**

The London specimen of *Archaeopteryx* BMNH 37001 is the only one of the seven known in which high resolution computed

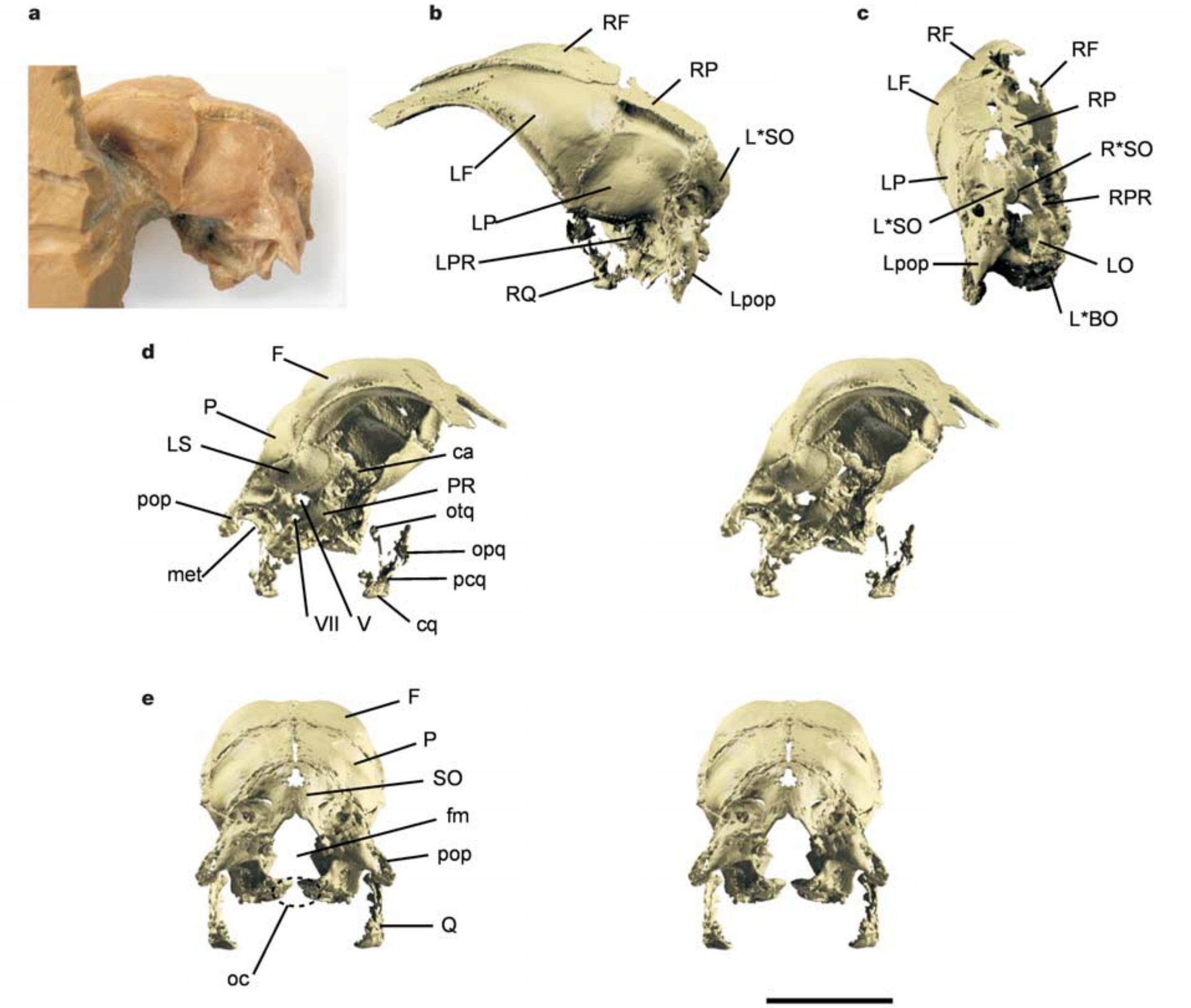

Figure 1 Braincase of the holotype of *Archaeopteryx lithographica* (BMNH 37001). Scale bar, 10 mm. **a**, Original prepared specimen in left lateral view[6]. **b**, **c**, 3D reconstructions of braincase based on X-ray CT data; left lateral view (**b**) and posterior view (**c**) showing right side collapse. **d**, **e**, Stereopair of restored braincase in oblique right-anterior view (**d**) and posterior view (**e**). Elements from the left side are reversed except for the right quadrate. L and R indicate left and right. Abbreviations: *BO?, ?basioccipital fragment; ca, crista arcuata; cq, mandibular condyle of quadrate; F, frontal; fm, foramen magnum; LS, laterosphenoid; met, metotic; O, opisthotic; oc, occiput; opq, orbital process of quadrate; otq, otic wing of quadrate; P, parietal; pcq, pterygoid condyle of quadrate; pop, paroccipital process of opisthotic; PR, prootic; Q, right quadrate; *SO, supraoccipital fragment; V, trigeminal nerve foramen; VII, facial nerve foramen. Original imagery available at < http://www.DigiMorph.org >.

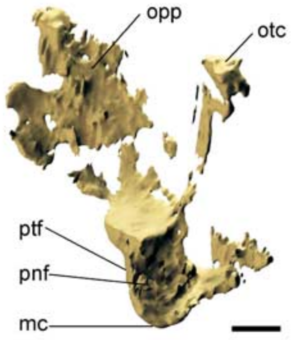

Figure 2 Right quadrate of BMNH 37001 in medial view. Scale bar, 1 mm. Abbreviations: ptf, pterygoid facet; pnf, pneumatic foramen; mc, mandibular condyle; opp, optic process; otc, otic capitulum. See also Supplementary Information for clear views of the pneumatic foramen.

tomography (CT) scanning[5] could be attempted because the braincase (Fig. 1a), including a partially exposed endocast (Fig. 1b), had been removed from the edge of the main specimen slab and prepared[6] in left lateral and posterior view to facilitate its description[7,8]. The right side of the braincase, still encased in matrix, is collapsed (Fig. 1c) and the floor is absent.

Our braincase reconstruction (Fig. 1d, e) shows that the frontals have an anterior articular facet for the nasals, and that the parietals, frontals and laterosphenoids meet in a blunt postorbital process. At this point, their margins are not clearly definable suggesting possible fusion. A crescentic fontanelle is present along the upper margin of the right crista arcuata. This is a vascular opening allowing the dural venous sinus (caudal petrosal sinus in avian literature) to drain out of the skull. Our reconstruction confirms that the previous identification of the opening on the occiput as the foramen for the external occipital vein[7,8] is correct. The foramen magnum is broad (40% of the total width of the brain) and triangular, in contrast to the smaller rounded shape reconstructed previously[7].

The right quadrate (Figs 1d and 2), hitherto unidentified and buried in the matrix, is almost in its original anatomical position. A similar quadrate was reported in the Munich specimen[9,10] and the morphology confirms that an isolated element previously reported in BMNH 37001 as a right quadrate[7] was incorrect, as suspected[10]; we suggest that it might be a sphenoid fragment. The form of the pterygoid articulation, at the limit of the CT resolution, appears to be rounded and therefore a condyle rather than a facet, which suggests a possibly mobile quadrate-pterygoid. The mesial face is perforated by a pneumatic foramen, positioned just dorsal to the mandibular condyle and just posterior to the pterygoid facet, that represents a previously unreported pneumatic cavity in *Archaeopteryx*. Witmer[11] considered quadrate pneumaticity to be a synapomorphy of at least carinate birds and the position of this foramen in *Ichthyornis* to be primitive for birds. Its presence in *Archaeopteryx* suggests it may be a synapomorphy at the avialan level. However, the distribution of quadrate pneumaticity in non-avian theropods is complex; it is present in a few groups including some maniraptorans (coelurosaurs with a bird-like flexible wrist) but is lacking in dromaeosaurids[12].

We have reconstructed most of the brain in three dimensions (3D) (Fig. 3). Previous models have necessarily relied on the surface details visible in BMNH 37001 (refs 13, 14) and other *Archaeopteryx* specimens, principally the Eichstätt and Munich individuals[9]. Pterosaurs, small coelurosaurs and birds have thin meninges and small venous sinuses so that the endocast of the braincase reflects precisely the brain anatomy and can be considered as an accurate index of the brain volume, mass and surface morphology[15–17].

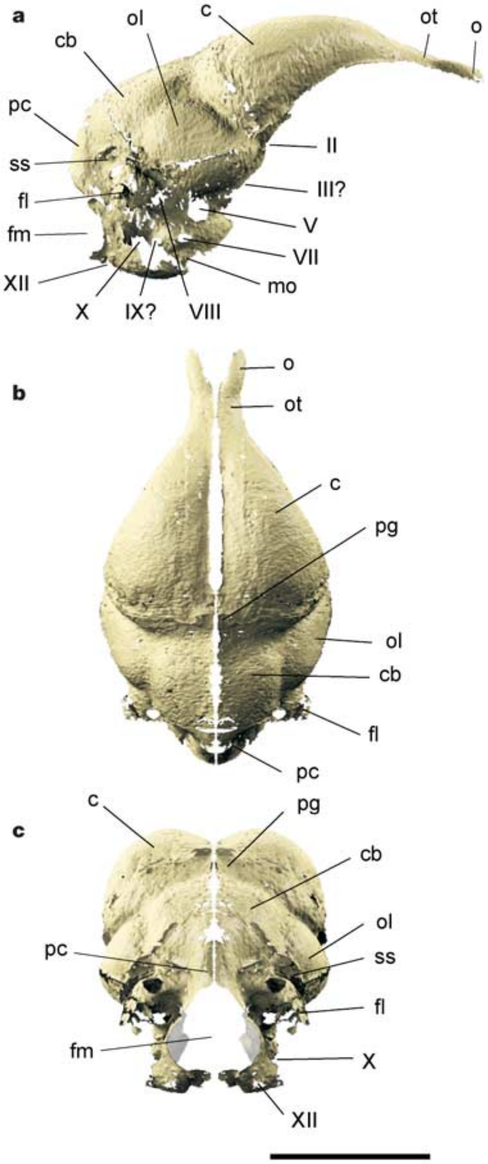

Figure 3 Restored endocast of the brain of BMNH 37001 rendered as a shell. Elements from the left side are reversed. Scale bar, 10 mm. **a**, Right lateral view. **b**, Dorsal view. **c**, Posterior view. Abbreviations: c, cerebrum (telencephalon); cb, cerebellum; fl, floccular lobe of the cerebellum; fm, foramen magnum; mo, medulla oblongata (rhombencephalon); o, olfactory lobe; ol, optic lobes (metencephalic tectum); ot, olfactory tract; pc, cerebellar prominence; pg, pineal gland (epiphysis); ss, semicircular sulcus. Cranial nerves: II, optic; III?, possible oculomotor; V, trigeminal; VII, facial; VIII?, auditory (or endolymphatic duct, see Fig. 5); IX?, glossopharyngeal; X, vagus; XII, hypoglossal. Original imagery available at < http://www.DigiMorph.org > .

The crescentic olfactory bulbs join the cerebral lobes by means of thick olfactory tracts. The cerebral hemispheres have a pyriform shape and contact the cerebellum dorsally across more than 64% of the total width of the brain. However, in comparison with modern birds, the cerebral hemispheres are less expanded and do not surround or envelope the olfactory tracts: the pineal gland emerges wedged between the lobes. The cerebellum is broad, being almost 50% of the total width of the brain. The optic lobes are large, globular to slightly pear-shaped, and laterally placed (and therefore well separated from each other); each is almost as large as the cerebellum. This pattern is shared with birds and, convergently, with pterosaurs[15,18,19]. In modern birds, the optic lobes are rotated posteriorly around their basal long-axes and therefore partly overlap the medulla oblongata[20]. In *Archaeopteryx* and *Enaliornis*[21], an Early

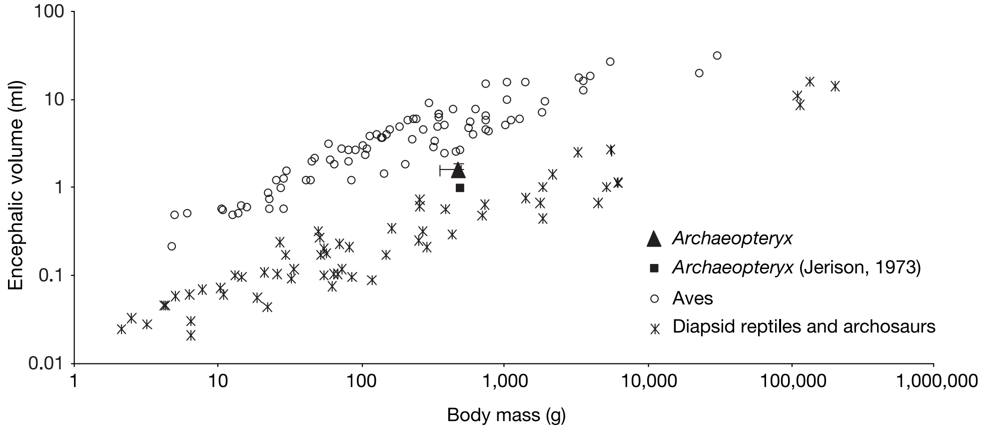

Figure 4 Encephalization index for birds, reptiles and BMNH 37001. Endoencephalic volumes of recent birds from ref. 17, brain masses for recent reptiles based on ref. 29; corrected to volumes using $\delta = 1.036\,\mathrm{g\,cm^{-1}}$ (refs 3, 17). Mass for BMNH 37001 based on mass = 468 g[10], horizontal error bar indicates masses from 350 g to 500 g and the estimation of Jerison[14]. See also Table 1 in Supplementary Information.

Cretaceous bird, the optic lobes are similar in shape but are positioned more anteriorly. The cerebral, cerebellar and optic fossae are smooth and converge in the anterior part of the parietal bone, and the boundaries are noticeable externally. The pineal fossa is not visible externally. The cerebellar fossa has no traces of foliar structures, probably owing to the presence of the occipital dural venous sinus. The semicircular sulcus (the depression beside the crista arcuata) surrounds the floccular lobe placed just anterior to the opisthotic. The relatively small hemispheres, lack of posterior rotation of the optic lobes and potentially relatively smaller cerebellum suggest that *Archaeopteryx* and *Enaliornis*[21] were more primitive than any modern bird.

The reconstructed 3D model of the brain encloses a volume of 1.4 ml. This must be considered as a minimum value because the base of the braincase is missing (around 88% of the total volume estimation). Previous estimates of relative brain size in *Archaeopteryx* varied by a factor of almost two, and it has remained contentious whether brain size increase was tied to the evolution of flight, arboreality, or other environmental influences[14]. We estimate the total volume to be around 1.6 ml, which is very near to Hopson's estimate of 1.76 ml (ref. 15). A plot of endocranial volume against body mass of some birds and modern reptiles (Fig. 4) places *Archaeopteryx* appreciably closer to birds than Jerison's estimate does[14]. Birds with the same body mass as *Archaeopteryx* have from one-third (for example, galliforms and columbiforms) to five times (for example, psittaciforms and passeriforms) bigger brains[14,15]. However, the brain of *Archaeopteryx* is about three times the volume of those of non-avian reptiles of equivalent size.

The right inner ear (Fig. 5) housed inside the right prootic and opisthotic elements is the better preserved, despite post-mortem rotational dislocation of both bones. The semicircular canals are not complete but their course and proportions can be established. The position of the anterior and lateral canals follows the archosaur pattern[22]. However, the anterior canal is considerably elongated and reflexed, and the course of the posterior canal extends ventrally below the plane of the lateral canal as in birds[22,23]. Moreover, the plane of the posterior canal is almost transverse at the common crus, which is therefore in a more posterior position than in non-avian archosaurs and non-archosaur reptiles[22,23]. The curved structure adjacent to the cochlea may represent the merged area of the vagal canal and metotic fissure.

We have plotted data for semicircular canal proportions and cochlea length (Fig. 6a, b) for selected birds, archosaurs and non-archosaur reptiles that place *Archaeopteryx* close to or within the range for modern birds (see Supplementary data), suggesting that

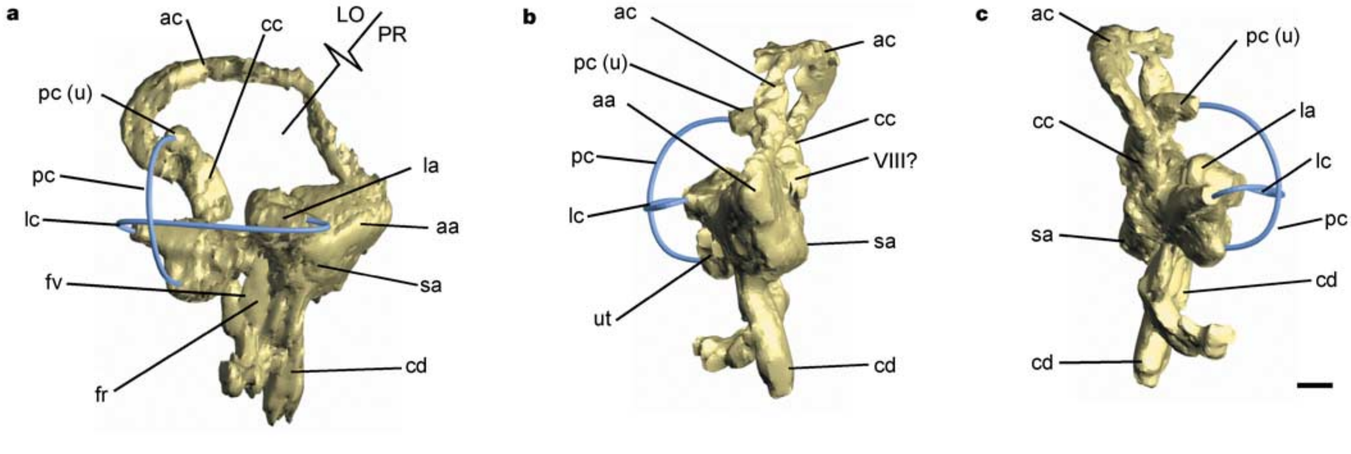

Figure 5 Right inner ear of BMNH 37001. 3D model based on X-ray CT. Scale bar, 2 mm. **a**, Lateral (external) view. **b**, Anterior view. **c**, Posterior view. Abbreviations: aa, anterior ampulla; ac, anterior canal; cc, common crus; cd, cochlear duct; fr, fenestra pseudorotunda; fv, fenestra vestibuli (fenestra ovalis); la, lateral ampulla; lc, tentative course of lateral canal; LO, left opisthotic; pc, tentative course of posterior canal; pc (u), posterior canal (upper part); PR, prootic; sa, sacculus; ut, utriculus; VIII?, acoustic nerve or endolymphatic duct. Original imagery available at < http://www.DigiMorph.org >.

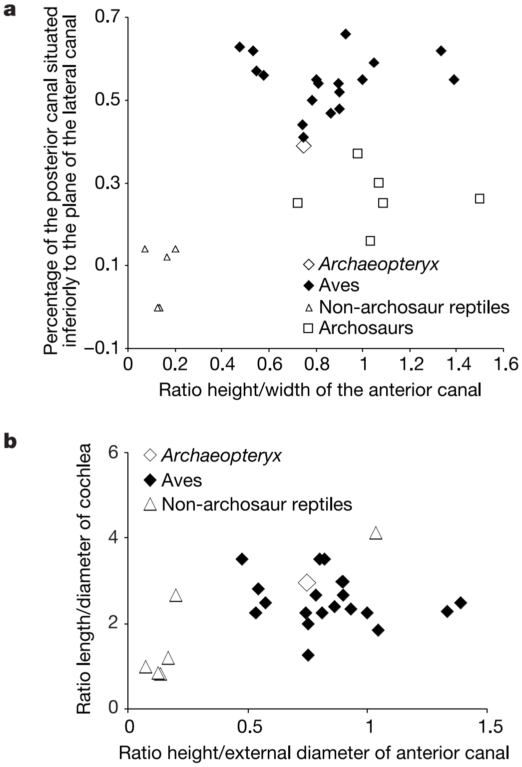

Figure 6 Comparative proportions of the inner ear of BMNH 37001, selected recent birds, archosaurs and non-archosaur reptiles. **a**, Anterior and posterior semi-circular canals. **b**, Length of the cochlea. All data on modern taxa were taken from ref. 23 (see also Supplementary Information) except *Alligator*[22]. For sources of data on fossil taxa see Table 2 in Supplementary Information.

the spatial sensory perception and auditory abilities of *Archaeopteryx* were similarly developed. The cochlea duct elongates in modern birds to enhance hearing ability[24] and offers an indication of the role of sonic stimuli in behavioural responses. This is much greater than in many other vertebrates and is associated with territorial, mating and feeding behaviour[25].

Few coelurosaurian dinosaur taxa preserve a brain endocast and most show the non-flexed plesiomorphic brain pattern with the optic lobes in dorsal position[18,26], except for *Troodon*[18] in which they are laterally placed; however, the cerebellum is comparatively much smaller than in *Archaeopteryx*. Maniraptorans do, however, show a trend towards brain enlargement and laterally separated optic lobes[27], with *Archaeopteryx* exhibiting a 'flight adapted' brain, a stage further towards the modern bird pattern. The remodelling of the brain towards the avian condition must have begun well before the appearance of *Archaeopteryx* 147 million years ago in the latest Jurassic. The convergent increase in visual and vestibular regions in pterosaurs[19] is further evidence that both an aerodynamic wing and a powerful central nervous system are integral to powered flight. □

Methods

The braincase of BMNH 37001 was scanned at the University of Texas at Austin's High-Resolution X-ray CT Facility. The specimen was scanned twice, at low and high X-ray energies (120 kV and 180 kV, respectively); the former accentuates compositional differences, whereas the latter is more noise-free and less prone to beam-hardening artefacts and interference from high-attenuation phases. The resulting serial sections were saved as two independent series of 1313 16-bit TIFF files. After a preliminary exploration, every second section of the low-energy data set was used to create 3D computer models of the objects by reconstructing the surfaces that connected corresponding outlines on adjacent sections[28]. The resulting matrix data size was $1,024 \times 1,024 \times 650$ voxels and the voxel size was $20 \times 20 \times 46\,\mu$m. The data set was segmented using Mimics v7.3 software (Materialise). Because of lateral changes and similarity in the X-ray attenuation values within the bone and limestone matrix, and the presence of highly attenuating manganese dioxide crystals, it was necessary to use local thresholds and work in the three orthogonal planes checking continuously the temporal 3D models of each bone as they were built up. Ogle (M. J. Gourlay, Northwestern Research Associates Inc.) and Simian v2 (University of Utah/Los Alamos National Laboratory) were employed for supplementary volume-rendering analysis.

The parameters common to both scan series were: X-ray spot size 0.030 mm; 1,024 detector channels; slice thickness and inter-slice spacing 0.0230 mm; field of reconstruction 21.0 mm; source to object distance 67 mm; source to detector distance 596 mm; 2,000 views; 200 ms acquisition time per view; acquired with 21 slices per rotation. Ring artefacts were corrected by R.A.K. using an original algorithm that processed the raw CT sinogram data to remove radially consistent channel-to-channel divergences, and resulted in no introduction of spurious features.

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Competing interests statement The authors declare that they have no competing financial interests.

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