Inferring echolocation in ancient bats

Arising from: N. Veselka *et al.* *Nature* 463, 939–942 (2010)

Laryngeal echolocation, used by most living bats to form images of their surroundings and to detect and capture flying prey[1,2], is considered to be a key innovation for the evolutionary success of bats[2,3], and palaeontologists have long sought osteological correlates of echolocation that can be used to infer the behaviour of fossil bats[4–7]. Veselka *et al.*[8] argued that the most reliable trait indicating echolocation capabilities in bats is an articulation between the stylohyal bone (part of the hyoid apparatus that supports the throat and larynx) and the tympanic bone, which forms the floor of the middle ear. They examined the oldest and most primitive known bat, *Onychonycteris finneyi* (early Eocene, USA[4]), and argued that it showed evidence of this stylohyal–tympanic articulation, from which they concluded that *O. finneyi* may have been capable of echolocation. We disagree with their interpretation of key fossil data and instead argue that *O. finneyi* was probably not an echolocating bat.

The holotype of *O. finneyi* shows the cranial end of the left stylohyal resting on the tympanic bone (Fig. 1c–e). However, the stylohyal on the right side is in a different position, the tip of the stylohyal extends beyond the tympanic on both sides of the skull, and both tympanics are crushed. In our opinion, the skull is too deformed to provide evidence of the spatial relationships of these bones in life. Micro-computed tomography (MCT) images of the skull make clear the extent of crushing and fragmentation (Fig. 1b, d). Veselka *et al.*[8] noted that the stylohyal–tympanic contact on the left side might be a taphonomic artefact, but nevertheless favoured the interpretation that *O. finneyi* was an echolocating bat. Available evidence indicates otherwise.

Four osteological traits have been postulated as indicators of laryngeal echolocation in bats: (1) an enlarged orbicular apophysis on the malleus[3,4]; (2) an enlarged cochlea[3–7]; (3) an enlarged paddle-like or bifurcated cranial tip on the stylohyal[3,4]; and (4) an articulation between the stylohyal and the tympanic[8]. Studies in other groups (for example, talpid moles[9]) indicate that large orbicular apophyses may occur in non-echolocating lineages, hence this trait cannot be considered a definitive indicator of echolocation[8]. However, the hypothesis that relative cochlear size is a good indicator of the echolocation abilities of bats[3–8] has not been refuted. The cochlea of *O. finneyi* falls outside the size range seen in living echolocating bats and is similar to the proportionally smaller cochleae of bats that lack laryngeal echolocation[4,8], suggesting that it did not echolocate.

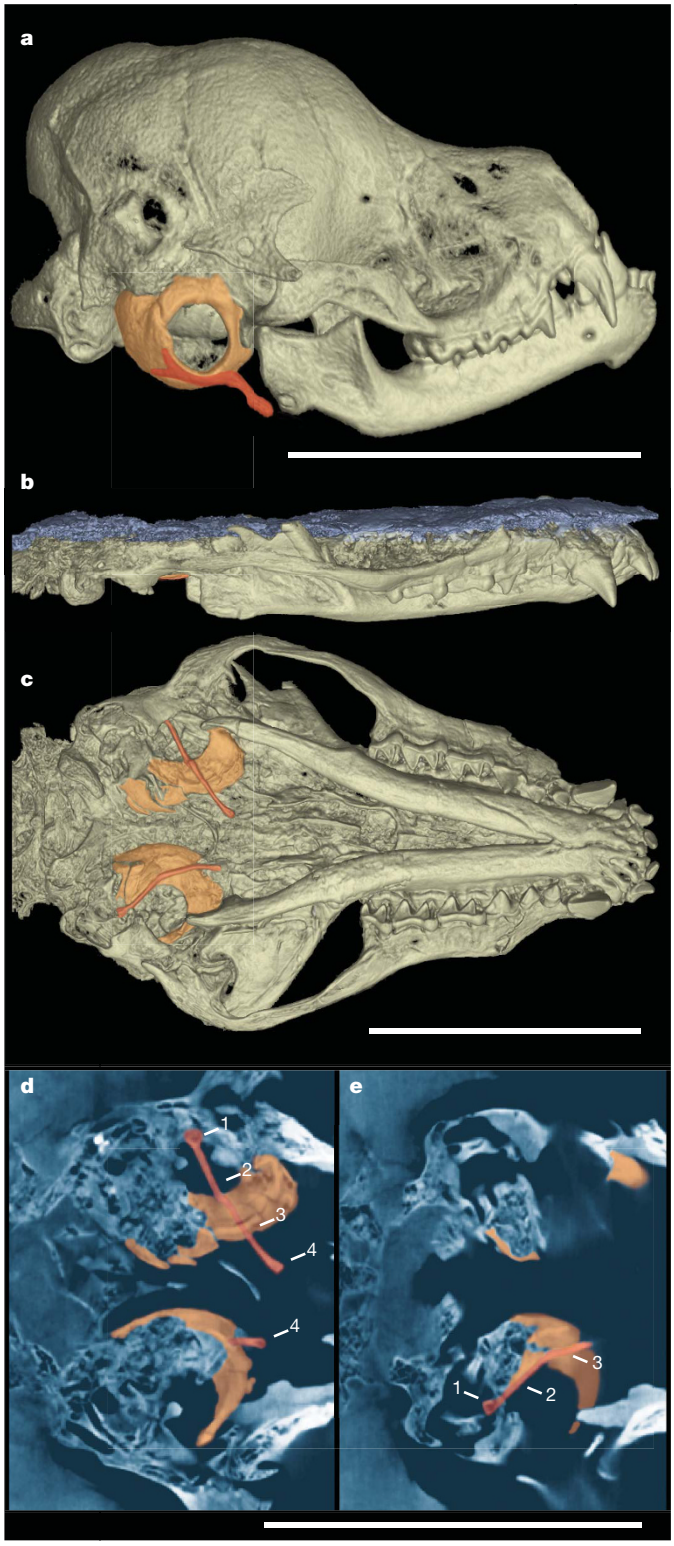

Figure 1 | Location and orientation of the stylohyal in an extant echolocating bat and in *O. finneyi*, as revealed by MCT scans. **a**, Lateral view of the skull of *Myzopoda aurita* (United States National Museum (USNM) 449282), an extant echolocating bat; note the depth of the braincase and ring-like tympanic (indicated in orange) where the stylohyal (red) articulates with the base of the skull. The cranial end of the stylohyal is expanded to form a bifurcated tip, and the stylohyal is fused to the tympanic along the length of its course across that bone. **b**, Lateral view of the skull of the holotype of *O. finneyi* (Royal Ontario Museum (ROM) 55351A). The cranium is crushed flat and lies directly under a thin, dense sediment layer (shown in blue). This layer is free of any sculptured bone fragments; the layers below it include multiple bone fragments that are all that remain of the braincase and rostrum roof. **c**, Ventral view of the same specimen (ROM 55351A). Both ear regions are preserved but crushed flat. The right and left stylohyals lie at different angles relative to the tympanic ring, indicating that neither was fused to the tympanic. **d**, **e**, Individual MCT slices through the basicranial region of the same specimen, with **d** through a plane slightly dorsal to **e**. The stylohyals are marked with numerals indicating thirds from the cranial end (1) to the distal end (4). The right stylohyal runs perpendicular to the tympanic and is fractured between points 2 and 3. The left stylohyal runs parallel to the edge of the tympanic ring (90° offset from the right stylohyal) and shows evidence of fractures between points 1 and 2, 2 and 3, and 3 and 4. Neither element shows unambiguous articulation with the tympanic or any other bone. Scale bars, 10 mm.

Data presented by Veselka *et al.*[8] indicate that cranial expansion of the stylohyal and an articulation between this structure and the tympanic are 100% correlated in extant bats. Previous reports that two families of echolocating bats (Nycteridae and Megadermatidae) lack stylohyal modifications[3,4,10,11] overlooked expansions of the stylohyal where it articulates with the tympanic. We found uniform presence of expansion and flattening of the stylohyal in both families. Observed correlations across all extant bat families indicate that this is a definitive marker of laryngeal echolocation, and that expansion and flattening of the cranial stylohyal should be considered a fundamental part of the stylohyal–tympanic articulation rather than an independent feature. In *O. finneyi*, the stylohyal is rod-like and has no cranial expansion or flattening other than a tiny knob at the proximal end. We hypothesize that this knob might be an ossified, fused typanohyal, which in some non-echolocating bats (for example, *Rousettus*, *Eonycteris*[12]) and insectivores (*Echinosorex*, *Erinaceus*[13]) is connected to the stylohyal by a thin ligament or cartilage; regardless, it is not comparable to the condition seen in any extant echolocating bat. In contrast with Veselka *et al.*[8], we conclude that *O. finneyi* did not have a stylohyal–tympanic articulation as it clearly lacks one of the definitive components of this feature: a modified stylohyal with an expanded and flattened cranial end.

Reconstructions of behaviours of extinct animals require careful consideration of preservation artefacts in fossils as well as patterns of form and function among extant animals. Our analyses show that the only two unambiguous pieces of evidence available at this time (cochlear size and stylohyal morphology) support the hypothesis that *O. finneyi* was not an echolocating bat. Because postcranial morphology indicates that *O. finneyi* could fly and phylogenetic analyses place it on the most basal branch within Chiroptera[4], the 'flight first' hypothesis for the origin of flight and echolocation in bats[3,4] remains the best-supported hypothesis for the origins of these key features.

METHODS

Micro-computed tomography (MCT) images of *O. finneyi* (Fig. 1b–e) were obtained with an MCT apparatus using a special 'region of interest' algorithm (RayScan 200 XE, RayScan Technologies). CT data for *Myzopoda aurita* (Fig. 1a) were provided by the University of Texas CT laboratory. Image processing was done with VGStudio MAX 2.0.1 (Volume Graphics).

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Veselka et al. *reply*

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We appreciate the comments of Simmons *et al.*[1] and welcome the new information they have provided about the oldest fossil bat, *Onychonycteris finneyi*, as well as their confirmation of contact between the stylohyal and tympanic bones in *Myzopoda aurita*, an extant laryngeal echolocator. Two skeletal features—relatively large cochleae and contact between the stylohyal and tympanic bones—identify extant bats with the capacity for laryngeal echolocation. Although the size of the cochlea can be measured in *O. finneyi*, the stylohyals may or may not have contacted the tympanics. Simmons *et al.*[1] disagree with our interpretation[2] of the possible contact between the stylohyal and the tympanic bone in *O. finneyi*, which indicated that this Eocene bat may have had the capacity for laryngeal echolocation, and have a different interpretation of our results.

We agree with Simmons *et al.*[1] that the known specimens of *O. finneyi* do not provide clear morphological evidence about contact between the stylohyal and tympanic bones and, by extension, about the applicability of this character for identifying this bats' capacity for laryngeal echolocation. As they note, the holotype of *O. finneyi* does provide data about the form of the stylohyal and the size of the cochlea, leading them to conclude that the bat did not echolocate.

Simmons *et al.* propose that the elongated stylohyal in bats is an ossified combination of stylohyal, tympanohyal and the ligament/cartilage between these two elements. The predictions arising from this hypothesis can be tested by studying patterns of development and ossification in living bats.

We join Simmons *et al.*[1] in awaiting the discovery and description of further fossil bats that can help to resolve the question of the origin and timing of the evolution of flight and echolocation in bats.

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