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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