CRITIQUES & DEBATES

Response to ‘Monotreme middle ear is not primitive for Mammalia’

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To date, a complete auditory apparatus (with malleus, incus, stapes, ectotympanic and perhaps surangular) is known for only three Mesozoic mammals, the haramiyidan Arboroharamiya allinhampsoni [1], the multituberculate Sinobaatar pani [2] and the zhangheotheriid Origolestes lii [3], with subsets of these bones preserved in a handful more, including the haramiyidan Vilevolodon diplomylos [4,5] discussed here. A goal of Wang et al. [5] was to evaluate the debate surrounding the various interpretations of these bones and to offer a cautionary tale about overinterpreting these structures. Because the new specimen of Vilevolodon reported by Wang et al. [5] preserved left and right mallei and incudes in articulation, these authors focused on the incudomallear joint. Wang et al. [5] found these two bones in Vilevolodon to be reminiscent of those in extant monotremes, with a relatively flat articulation between a plate-like incus and similarly thin mallei. On the strict consensus tree from their parsimony analysis, Wang et al. [5] optimized five characters of the incudomallear articulation and reported that the character states associated with the overlapping incudomallear articulation of extant monotremes and Vilevolodon optimized as primitive for Mammalia. However, they expressed uncertainty as to whether this overlapping joint evolved convergently in haramiyidans and monotremes or was an innovation at the level of Mammalia.

Meng and Mao [6] question Wang et al.’s [5] identification of the incus in the new specimen of Vilevolodon, because it differs from that reported for the holarcctic type [4]. Wang et al. [5] addressed this already, noting that the two incudes have the same shape, with the only difference being the interpretation of the incudomallear joint. Meng and Mao [6] then conduct an optimization employing different criteria (their Fig. 1o) from those of Wang et al. [5]. Rather than optimizing the five characters individually, as had Wang et al. [5], Meng and Mao [6] lump the five into two broad morphologies: overlapping and partial overlapping joints (their braced hinge joint). They report that it is more parsimonious to have the partial overlapping joint as primitive for Mammalia, which they state falsifies Wang et al.’s hypothesis. Meng and Mao [6] illustrate what they consider to be the Wang et al. [5] hypothesis in their Fig. 1n, but we emphasize that this was not an analysis that was ever conducted by the latter authors.

Wang et al. [5] did not figure any of their five individual optimizations. We revisit them here, illustrating results for two in Fig. 1a and b. We made amendments to the protocol of Wang et al. [5] based on concerns raised by Meng and Mao [6]. First, we added scores for S. pani; Wang et al. [5] did not score S. pani for the 509 morphological characters in their taxon-character matrix as little of the anatomy of this taxon beyond the ear ossicles was reported [2]. Second, we modified scores for the haramiyidans Arboroharamiya (regarding the shape of the incudal body) and Qishou (which was changed to unknown for all incudomallear characters), following Meng and Mao [6]. Wang et al. [5] suggested that Qishou (based on an image in [7]) had an incus and malleus much like that in Vilevolodon. Meng and Mao [6] include two computerized tomography (CT) slices of Qishou (Fig. 1k and l) that clearly show there is only one bone present. We acknowledge the error in interpretation by Wang et al. [5]. However, rather than an incus preserved on the malleus in Qishou, based on these new cross sections, we interpret this as the malleus with a facet for the incus, still resembling the condition in Vilevolodon. Nevertheless, we score Qishou as unknown here. Third, we eliminated the optimization of character 416, the alignment of the malleus and incus, because evaluation of this character requires knowledge of the plane of the ectotympanic, which is seldom preserved in fossils.

The first illustrated optimization is of character 417 from Wang et al. [5] (Fig. 1a), the shape of the incudal body, the part in contact with the malleus. We scored this as a trochea in the outgroup Morganucodon, plate-like in most Mesozoic mammals, and globular in the extant therian Philander and Arboroharamiya, following Meng and Mao [6]. Wang et al. [5] suggested that the incus of the Zhangheotheriid Origolestes had a thickened body and scored it as globular. We changed their score of Origolestes to plate-like; Meng and Mao [6] have provided a new CT slice of Origolestes (their Fig. 1i), which shows an incudal body more reminiscent of that in the monotreme Tachyglossus (their Fig. 1e) than in the marsupial Didelphis (their Fig. 1g). In our optimization (Fig. 1a), the plate-like incus is primitive for Mammalia with the globular state derived independently in

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Philander and Arboroharamiya. We found similar results for the amended optimizations for characters 415 and 418 (the geometry and orientation of the incudomallear joint, respectively), that is, the states associated with the condition in Vilevolodon and monotremes are primitive for Mammalia.

Character 419 concerns the extent of overlap between the malleus and incus, complete or partial, which is applicable only for taxa with the incudomallear articulation in the same plane as the malleal body—character 418), on simplified consensus tree, with the primitive condition ambiguous for Mammalia (see Supplementary Data online for terminology and abbreviation). (c) and (d) Isosurfaces from CT scan of the ex tant monotreme Ornithorhynchus anatinus, Carnegie Museum 50815; (c) malleus (red), incus (green), stapes (purple) and ectotympanic (light blue) in oblique posterodorsal view; (d) malleus (red) with black arrows on low ridge marking the border of the incudal facet and asterisk in the concave part of the incudal facet.

Figure 1. (a) Optimization of character 417 from Wang et al. [5], the shape of the incudal body, on simplified consensus tree, with plate-like identified as primitive for Mammalia. (b) Optimization of character 419 from Wang et al. [5], extent of overlap of malleus and incus (only applicable for taxa with the incudomallear articulation in the same plane as the malleal body—character 418), on simplified consensus tree, with the primitive condition ambiguous for Mammalia (see Supplementary Data online for terminology and abbreviation). (c and d) Isosurfaces from CT scan of the ex tant monotreme Ornithorhynchus anatinus, Carnegie Museum 50815; (c) malleus (red), incus (green), stapes (purple) and ectotympanic (light blue) in oblique posterodorsal view; (d) malleus (red) with black arrows on low ridge marking the border of the incudal facet and asterisk in the concave part of the incudal facet.

malleus has a low ridge that marks the edge of the incudomallear joint surface (arrows in Fig. 1d) and a joint surface that is partially concave (asterisk in Fig. 1d), both morphologies expressed in the partial overlapping joint. Transforming the condition of the platypus into the partial overlapping joint requires a posterior shift of the incus with respect to the malleus and a more pronounced ridge marking the incudomallear joint surface. These morphologies represent the first steps in the transformation of the load bearing trochlear joint between the quadrat (incus) and articular (malleus), as occurs in Morganucodon [8], for example. No matter what the direction of the transformation of the overlapping and partial overlapping joints may have been, it likely occurred more than once in mammal evolution, as the postdentary bones detached multiple times from the lower jaw [8].

SUPPLEMENTARY DATA

Supplementary data are available at NSR online.

Conflict of interest statement. None declared.

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