

## Comment on “Independent Origins of Middle Ear Bones in Monotremes and Therians” (I)

The middle ear ossicles of all extant, adult members of crown-group Mammalia (1) are homologous with a series of bones in the lower jaw of nonmammalian amniotes (2, 3). Rich *et al.* (4) recently proposed that the structurally complex mammalian ear evolved independently in the monotreme and therian lineages. This conclusion is based on a newly discovered specimen (NMV P212933) that provisionally was referred to *Teinolophos trusleri* and that exhibits a distinct mandibular trough. Without questioning the validity of their morphological observations, we assert that at least three hypotheses can be formulated based on the information provided by Rich *et al.* Only one of these hypotheses supports the independent origin of the mammalian ear in the absence of a phylogenetic analysis. Considering that the mammalian middle ear is one of the best known morphological transformations in vertebrate history, alternative hypotheses must be explored.

The first possible hypothesis is that the taxonomic referral of the new specimen by Rich *et al.* is correct (i.e., NMV P212933 and the holotype of *T. trusleri* represent the same species), and *T. trusleri* is a member of the monotreme lineage. The taxonomic referral is based largely on a heavily worn tooth [figure 2, G and H, in (4)] that was associated with, but not attached to, the mandible of NMV P212933. Because Rich *et al.* present no new analysis, the phylogenetic position of *T. trusleri* on the monotreme lineage is based on the conclusions of previous phylogenetic analyses (5–8); however, these analyses include only the holotype of *T. trusleri* and score it as lacking a mandibular trough. This first hypothesis supports the dual origin of the mammalian middle ear but requires that some individuals of *T. trusleri* have a fully transformed adult mammalian ear, whereas others do not. A single species polymorphic for the mammalian middle ear seems biologically unlikely.

A second hypothesis is that NMV P212933 and the holotype of *T. trusleri* represent the same taxon, and the holotype has an unreported mandibular trough. This hypothesis requires that all earlier published descriptions and discussions of the holotype (5–10) incorrectly assessed the morphology of the holotype. Because the monotreme affinities of *T. trusleri* were based on analyses that scored this taxon as lacking a mandibular trough (5–8), this hypothesis also requires that the phylogenetic position of *T. trusleri* be reanalyzed before a dual origin of the mammalian ear can be justified.

A third hypothesis is that NMV P212933 and the holotype of *T. trusleri* are not the same taxon. Accepting this hypothesis requires that the holotype and NMV P212933 be scored as separate terminal taxa in a phylogenetic analysis. This alternative is the most conservative, considering the requirements forced by the first two hypotheses and the fact that numerous morphological differences, in addition to the presence or absence of a mandibular trough, appear to exist between the holotype and NMV P212933. For example, based on the images shown in figure 2 in (4), the inflection of the angular process, height of the angular process relative to the horizontal ramus, relative position of the mandibular foramen, sizes of the ultimate and penultimate alveoli, presence of a fused coronoid, and overall shape of the jaw (especially along the ventral margin) differ considerably between these specimens. A more conservative approach also questions a taxonomic referral based on a heavily worn tooth that was associated with, but not attached to, the mandible of NMV P212933. Furthermore, the preserved teeth of the holotype and NMV P212933 represent different positions within the tooth row, complicating strict comparison. If one adopts this approach, accepting the combination of characters illustrated in figure 3C in (4) is not justified.

If morphological evolution is to be interpreted by using a phylogenetic framework, then the systematic position of specimens pertinent to that interpretation must be based on derived characters. Presumptions of systematic affinity based on overall similarity or the possession of “characteristic” features can be misled by the influence of plesiomorphic morphology. Unfortunately, the polarity of the features seen in NMV P212933 that Rich *et al.* use to characterize monotremes is yet to be established and therefore cannot currently be considered diagnostic (11). The importance of NMV P212933 to our understanding of morphological evolution in Mammalia warrants that no assumptions be made regarding its phylogenetic position. We therefore advocate that a phylogenetic analysis including NMV P212933 and the holotype of *T. trusleri* as distinct terminal taxa be conducted before accepting any hypothesis proposing homoplastic transformation of the mammalian middle ear.

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