

## Response to Comments on “Independent Origins of Middle Ear Bones in Monotremes and Therians”

We stand by our assessment of the taxonomic identity of *Teinolophos trusleri* and maintain that this specimen shows features that support an independent evolution of the middle ear in living monotremes and therians. Bever *et al.* (1) question whether the lower jaw that we (2) provisionally referred to *T. trusleri* (NMV P212933) can be conspecific with the holotype jaw (NMV P208231), in part because the latter appears to lack the mandibular trough preserved in the referred specimen. Our reexamination of the holotype (Fig. 1A), in light of knowledge gained from NMV P212933 (Fig. 1B) and other more fragmentary specimens, indicates the presence of an indentation bounded above by a slight ridge in the position of the internal trough seen in other specimens. Therefore, we are confident that the type also possesses a mandibular trough, although it has been nearly obliterated by diagenetic crushing and distortion. This was implicit in our statement about the damaged (hence, unreliable) nature of the type with regard to this feature (2). The suggestion by Bever *et al.* (1) that the holotype is a mature individual in which the trough seen in the younger referred specimen was lost ontogenetically is, therefore, not supported.

Some of the other differences between the holotype and the referred specimen cited by Bever *et al.* are also due to damage of the former, although some proportional differences between the two specimens appear to be real. The lack of complete morphological identity between these specimens was why we considered their attribution to the same species to be “provisional” [note 24 in (2)].

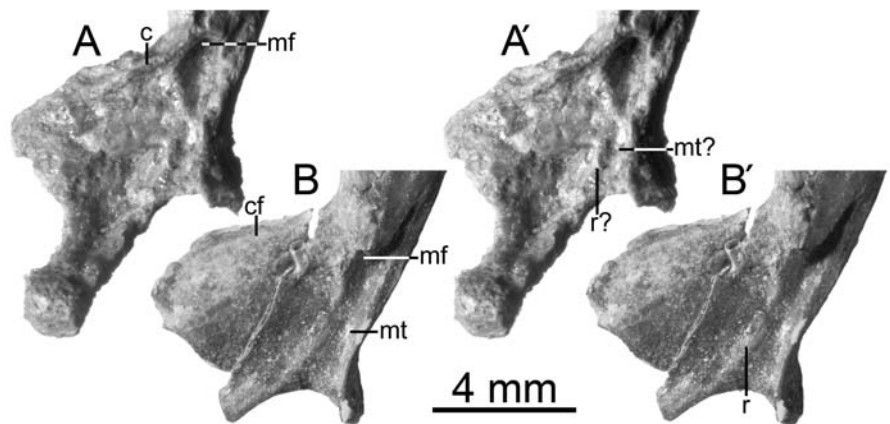
Bever *et al.* question the monotreme affinities of *T. trusleri* and, therefore, the “dual origin of the mammalian middle ear,” because they “were based on [prior] analyses that scored this taxon as lacking a mandibular trough” (1). At our request, Springer reanalyzed the phylogenetic position of *T. trusleri* using the data matrix published in (3), with the character “postdentary trough” rescored in *Teinolophos* as present rather than absent. A strict consensus tree of six trees of 334 steps (one more than in the original analysis) contains a monophyletic Monotremata comprising *Teinolophos*, *Ornithorhynchus*, *Obdurodon*, and *Steropodon*.

The molar tooth associated with the referred specimen, although heavily worn, closely resembles that of the holotype in having the characteristic derived bilophodont pattern present in *Steropodon* and ornithorhynchids but notably absent in other Mesozoic mammals. The association of this tooth with the referred jaw was made because it was found next to the mandible, close to the alveoli containing broken roots, into which it fits perfectly. Furthermore, only one other isolated mammalian tooth has been found at Flat Rocks since 1997, although 37 mammalian jaw fragments have been collected. Thus, we are confident that the referred specimen NMV P212933 is a monotreme congeneric with *Teinolophos* and that it very likely pertains to *T. trusleri*.

Rougier *et al.* (4) do not challenge the identification of *Teinolophos* as a monotreme, but do question our interpretation (2) of its mandibular trough as housing postdentary bones homologous with mammalian middle ear bones. They argue that (i) the mandibular trough does not possess the features characteristic of mammaliaforms with known postdentary bones; (ii) the flat surface on the floor of the trough lacks features expected of a contact facet for the angular bone (homolog of mammalian ectotympanic); and (iii) our preferred phylogenetic hypothesis regarding the position of monotremes with respect to other mammals lacks supporting data.

Our interpretation of the mandibular trough in *Teinolophos* as the site of a rod of postdentary jaw bones is based entirely on its resemblance to a similar trough in the geologically older mammaliaforms *Morganucodon*, in which postdentary bones have been found in place (5), and *Haldanodon*, to which an isolated postdentary rod is convincingly attributed (6). The trough in all three taxa extends between the mandibular foramen and the notch above the angular process and is bounded above by a distinct ridge, more prominent in the basal mammaliaforms than in *Teinolophos*. The ridge in all three taxa also has a low area just behind the raised facet for the coronoid bone, thought to allow the mandibular branch of the trigeminal nerve to pass into the anterior part of the trough and forward into the mandibular canal. This nerve would not normally contact the mandible farther posteriorly, so it does not explain the existence of the posterior part of the trough in *Teinolophos*.

Rougier *et al.* (4) do not comment on these resemblances. Rather, they argue that the trough in *Teinolophos* is not homologous with that in basal mammaliaforms because it does not continue posteriorly on to the condylar process as a well-defined groove bounded above by a continuation of the medial ridge [see figure 3, A and B, in (2)]. However, whereas the grooved condylar process in *Morganucodon* and *Haldanodon* lies directly behind the trough (5, 7), the preserved base of the condylar process in the undistorted NMV P212933 [figure 2E in (2)] curves laterally from the plane of the trough; consequently, the postdentary rod appears to have lost its primitive contact with the condylar process. This evidence of increased transverse separation of the middle ear bones from the jaw joint



**Fig. 1.** (A and A') Stereophotographic medial view of the posterior part of the holotype mandible of *T. trusleri*, specimen NMV P208231. (B and B') Stereophotograph of the posterior part of the mandible of referred specimen of *T. trusleri*, NMV P212933. c, coronoid; cf, coronoid facet; mf, mandibular foramen; mt, mandibular trough; mt?, probable mandibular trough; r, ridge; r?, probable ridge.

is to be expected in the transition to free ear bones, as we argued with respect to the presumed angular facet (2). Thus, we do not consider the differences noted by Rougier *et al.* to be valid arguments against the trough in *Teinolophos* being homologous with that of basal mammaliaforms.

We interpreted a flat longitudinal surface on the floor of the trough in *Teinolophos* as a possible contact facet for an accessory jaw bone. Rougier *et al.* deny that this surface is a contact facet inasmuch as “[i]t has no limits, no textural changes, and no indication of a conspicuous area for articulation” (4). In fact, the surface is delimited medially by the sharp ventromedial border of the trough and laterally by a distinct angle with the curved lateral wall of the trough, seen in all well-preserved specimens. Its posterior termination is also marked by a change in surface contour. We do not think that such a surface needs to show a distinct texture or conspicuous area for articulation to be a contact facet. Nor do we accept that the surface “is merely the floor of the large mandibular canal” (4), for we fail to see how the mandibular nerve or other soft tissues could create such a distinctly flattened area. We think that a bone with a flat ventral surface is its most likely cause, which, based on comparison with early mammaliaforms, would be the angular.

That the putative angular facet extends forward into the mandibular canal of the dentary is unlike the angular facet of known mammaliaforms, and we cannot explain why it does so in *Teinolophos*. Our suggestion that it was “possibly associated with the great enlargement of the mandibular foramen” (2) was meant to indicate how such a configuration might have been permitted, not what its functional or developmental cause might have been. These remain unknown.

Rougier *et al.* (4) consider our statement regarding the position of monotremes with respect to other mammals to lack supporting data and imply that our choice of cladograms was made to fit our prior conclusion of an independent origin of free ear bones in monotremes and therians. The evidence we adduced

for a polyphyletic origin of the definitive mammalian middle ear bones, i.e., ear bones freed from the lower jaw, was based on *Teinolophos* being a monotreme, which is generally accepted, and on marsupials and placentals being more distantly related to living monotremes than is *Teinolophos*. We noted in our original report that “[t]he current consensus of molecular and morphological analyses places monotremes outside of a monophyletic Theria” (2). These relations, as expressed in figure 4 in (2), are the basis for our claim of a polyphyletic origin of free middle ear bones in mammals. Our reason for selecting the phylogeny advocated by Rowe (8), in which all other Mesozoic mammals lie closer to Theria than to Monotremata, was that it “requires the least amount of homoplasy in comparison with other proposed phylogenetic placements of monotremes” (2).

Finally, Rougier *et al.* state that our tree does not support our claim of a polyphyletic origin of free ear bones, “because upon optimization, the character ‘free middle ear bones’ is equivocal at the base of Monotremata and present at the root of Mammalia” (4). This is incorrect, because this character is also equivocal at the root of Mammalia. Two equally parsimonious outcomes (each involving two evolutionary steps) are possible: Either free ear bones originated once, at the base of Mammalia, with a subsequent reversal to the attached state in *Teinolophos*, or free ear bones originated independently in post-*Teinolophos* monotremes and other mammals (Theriimorpha) [figure 4 in (2)]. We consider it unlikely on functional grounds that ear bones once freed from attachment to the mandible would revert to the primitive attached condition. Discovery of new Mesozoic monotremes will test this hypothesis.

When the problems in interpreting the damaged holotype specimen are taken into account, we are confident that our conclusions on the taxonomic identity and jaw morphology of *T. trusleri* are substantially correct and that our interpretation of a polyphyletic origin of the definitive mammalian middle ear best explains the available evidence.

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#### References and Notes

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