



## Invited reply

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# In defence of comparative physiology: ideal models for early tetrapods do not exist

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We thank Anderson *et al.* [1] for engaging in our paper on hearing in salamanders [2]. We have written our paper primarily as experimental physiologists basing hypotheses on recent animals and with no research expertise in palaeontology. Therefore, discussions with palaeontologists are especially welcome. In many ways, palaeontology should constrain our hypotheses and the finding of a fossil tympanate urodele, for example, could change our views, as could more information on the ear region of the early tetrapods. It is also true that comparative physiology has erred in its ways previously—by comparing disparate living exemplar species and inferring that such a lineup reflects evolutionary history (i.e. naming recent species as ‘lower’, ‘primitive’ or ‘ancestral’). A stellar example is the older view of the tympanate ear originating in the tetrapod ancestors with the recent groups—*anurans*, *lizards*, *archosaurs* and *mammals* exemplifying different stages in the evolution of the middle ear. This view has been abandoned, based on the thorough palaeontological investigations by Clack [3,4] and others showing independent origins of the tympanate ear in all the major groups.

When this is said, we find the criticism to be misdirected concerning two major points, the first being the use of model animals. Anderson *et al.* state that ‘Salamanders are not evolutionary intermediates’ and with that we fully agree; we certainly do not regard salamanders or any other living creatures as evolutionary intermediates, ‘missing links’ or even as ‘exemplar species’. Furthermore, to designate any living species as ‘exemplar’ seems to us to revert to the practices described above—any living species will only be superficially similar to the ancient species and may, in the best case, illustrate some aspects of its physiology. Rather, the solid comparative approach would be to investigate many recent species (i.e. to compare the physiology of salamanders, caecilians and earless frogs and infer ancestral physiology from common features). Another strategy in comparative physiology is to use living organisms to investigate biological solutions to problems common to fossils and (unrelated) recent animals—for example, to use large mammals as models for large dinosaurs. Anderson *et al.* claim that salamanders are an inappropriate model, because ‘there is strong evidence that salamanders have secondarily lost a tympanic ear’ and this ‘dramatically changes the interpretation of the results of’ our study [2]. Now, it is probable that salamanders are secondarily reduced, also in their middle ear configuration, but it is by no means certain that their ancestors were tympanate. This is most likely under the *temnospondyl* hypothesis; under the *lepospondyl* hypothesis, the divergence-dating by Pyron [5] suggests a caudate–*anuran* split at 292 Ma, long before the atympanate proanuran *Triadobatrachus*, and so making a tympanate ancestry of salamanders much less likely. However, even if the salamanders are secondarily reduced from tympanate ancestors they could still be models of how a tetrapod would hear with a non-functional middle ear—most likely the

middle ear would revert to the ancestral state, which in our view would be a non-tympanic middle ear and an inner ear with a patch of sensory epithelium without otolith covering. Further, Anderson *et al.* claim that salamanders are an inappropriate model because they have a long history of terrestrial hearing, but a main point in our paper is precisely that *there is no living terrestrial animal 'without any evolutionary history of terrestrial hearing'*—even with a non-tympanic ear, animals are still able to hear airborne sound, at least in the low-frequency range, where hearing, also in tympanate frogs, is extratympanic [6]. In addition, whereas it is true that the auditory system of any recent species may have been sharpened by many millions of years of natural selection since the early tetrapods, its physiology still reflects what a non-tympanic ear can do, maybe in a somewhat ideal situation. Thus, it is not clear what Anderson *et al.* would suggest to do instead: are there better models around for hearing of early tetrapods (apart from fossils)? We are not really free to choose models, if we are working with living organisms. There are not many other choices than urodeles or caecilians, if we wish to investigate hearing in atympanate tetrapods. Similar criticism could be used against using lungfish as a model of anything related to

tetrapods—recent lungfish are also secondarily reduced and have approximately 400 Ma of independent evolutionary history, but it is (in our opinion) the best choice for a model for very early tetrapod hearing.

Second, lissamphibian ancestry is not as universally agreed upon as Anderson *et al.* claim when favouring the temnospondyl hypothesis. We concede that we might have understated the current phylogenetic debate in clearly siding with the 'heterodox' lepospondyl hypothesis, but in addition to the paper by Marjanović & Laurin [7] cited by Anderson *et al.* it is backed by the recent (in our opinion) authoritative papers by Pyron [5] and Pyron & Wiens [8] based on large-scale molecular analysis of recent taxa and incorporating fossil data. However, to reiterate our first point, we note that this aspect of the phylogeny is not really relevant to the paper and its main conclusions about hearing with a non-tympanic ear. Finally, one really important functional element of the lissamphibian non-tympanic ear—the operculum—in our opinion must pre-date the tympanic ear. The operculum has not been clearly identified in any of the lissamphibian putative ancestors—except maybe in microsaurians [9, p. 163–164]. This is another reason why salamanders are interesting as models for hearing in the ancestral tetrapods.

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