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environmental stimulations and one with high-frequency aerial sound. Salamanders show a phylogenetically correlated reduction in innervation of the epithelium associated with high frequency sound perception [22], indicating the presence of a tympanic hearing system in their evolutionary past. A similar trend is found in the atympanic caecilians [23,24]. This point is critical because Christensen et al. tested sensitivity to sound vibrations at the auditory nerve, which directly reflects the innervation of the sensory epithelia detecting the stimulus. Because salamanders have remnants of the greater innervation of the fully tympanic ear, it is expected that they can perceive sound better than animals
without any evolutionary history of terrestrial hearing. The fact that secondarily aquatic salamanders, such as axolotl, do not differ in their ability to hear aerial sound from terrestrial salamanders reflects the conservation of a degree of terrestrial hearing capability. Even under the heterodox ‘lepospondyl hypothesis’ [18] this loss is recognized.

2. Microsaurs are not representative of early tetrapods

Christensen et al. [1] assert that microsaurs are morphological exemplars for the early tetrapod condition (a rationale for this was not provided) and that similarities of the middle ear can be used to associate the functional data derived from salamanders with the early evolution of frog-like hearing. This is problematic for two reasons. First, phylogenetically microsaurs are more closely related to the amniote crown group than any early tetrapod [5,11,24,25]. They are derived in both lacking a spiracular embayment and in possessing a short, robust stapes, unlike all taxa that span the water-to-land transition up to, and including, frogs (figure 1). Rather than representing a transition between aquatic and terrestrial living, microsaurs are highly specialized terrestrial species adapted to burrowing.

Second, whereas Christensen et al. are correct in recognizing superficial similarities between salamanders and microsaurs, including the lack of an otic notch and stapes with broad footplates and short columellae, microsaurs differ in several important anatomical details [26–28]. For example, microsaurs have the stapes completely filling the fenestra vestibularis, whereas salamanders also have an operculum [22]. All lissamphibians [24,29] and some temnospondyls [19] possess a posterior pressure relief pathway via the perilymphatic foramen, whereas microsaurs possess an ossified crista interfenestralis that prevents this posterior perilymphatic flow, strongly suggesting they possess a more amniote-like anterior pattern [26,30].

3. Conclusion and recommendations

Experimental studies of modern taxa have the potential to inform our understanding of major transitions in evolutionary history otherwise preserved only in the fossil record, but the selection of exemplary taxa for such studies is non-trivial to their applicability. Researchers must consider the evolutionary histories of taxa to ensure that the model organisms are appropriate analogues so that conclusions can be drawn with confidence. The middle ear of Polypterus is more anatomically similar to that seen in stem tetrapods and lungfish near the tetrapodomorph divergence and could be an appropriate analogue to test in future studies of this question.

Given the above, we assert that the conclusion that ‘early tetrapods also may have been able to detect aerial sound before the appearance of the tympanic middle ear’ ([11], p. 8) drawn from observations of salamanders and microsaurs is unfounded. Instead, the results of this study provide interesting insights into the strength of the conservation of an auditory apparatus adapted to terrestrial hearing in a group of aquatic salamanders.

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References


