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Modes of ventilation in early tetrapods: Costal aspiration as a key feature of amniotes

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The key difference between amniotes (reptiles, birds and mammals) and anamniotes (amphibians in the broadest sense of the word) is usually considered to be the amniotic egg, or a skin impermeable to water. We propose that the change in the mode of lung ventilation from buccal pumping to costal (rib-based) ventilation was equally, if not more important, in the evolution of tetrapod independence from the water. Costal ventilation would enable superior loss of carbon dioxide via the lungs: only then could cutaneous respiration be abandoned and the skin made impermeable to water. Additionally efficient carbon dioxide loss might be essential for the greater level of activity of amniotes. We examine aspects of the morphology of the heads, necks and ribs that correlate with the mode of ventilation. Anamniotes, living and fossil, have relatively broad heads and short necks, correlating with buccal pumping, and have immobile ribs. In contrast, amniotes have narrower, deeper heads, may have longer necks, and have mobile ribs, in correlation with costal ventilation. The stem amniote *Diadectes* is more like true amniotes in most respects, and we propose that the changes in the mode of ventilation occurred in a stepwise fashion among the stem amniotes. We also argue that the change in ventilatory mode in amniotes related to changes in the postural role of the epaxial muscles, and can be correlated with the evolution of herbivory.

Key words: Amniotes, amphibians, skull, ribs, ventilation, carbon dioxide, Palaeozoic, herbivory.

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