Origin of the unique ventilatory apparatus of turtles

Tyler R. Lyson (1, 2, 3)*, Emma R. Schachner (4, 5), Jennifer Botha-Brink (6, 7), Torsten M. Scheyer (8), Markus Lambertz (9), G. S. Bever (10, 11), Bruce Rubidge (3), Kevin de Queiroz (2)

(1) Department of Earth Sciences, Denver Museum of Nature and Science, Denver CO, USA; (2) Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC, 20560, USA; (3) Evolutionary Studies Institute, University of the Witwatersrand, PO Wits 2050, Johannesburg, South Africa; (4) Department of Veterinary Clinical Sciences, School of Veterinary Medicine, Louisiana State University, Baton Rouge, LA 70803; (5) Department of Biology, University of Utah, Salt Lake City, UT 84112; (6) Karoo Palaeontology, National Museum, Box 266, Bloemfontein, 9300, South Africa; (7) Department of Zoology and Entomology, University of the Free State, Bloemfontein, 9300, South Africa; (8) Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland; (9) Institut für Zoologie, Rheinische Friedrich-Wilhelms-Universität Bonn, Poppelsdorfer Schloss, 53115 Bonn, Germany; (10) New York Institute of Technology, College of Osteopathic Medicine, Old Westbury, NY 11568; (11) Division of Paleontology, American Museum of Natural History, New York, NY 10024.

*Correspondence author email. *tyler.lyson@dmns.org*

Background. The turtle body plan differs markedly from that of other vertebrates and serves as a model system for studying structural and developmental evolution. Incorporation of the ribs into the iconic turtle shell negates the rib movements that effect lung ventilation in the majority of air-breathing amniotes (the clade encompassing mammals, lizards, turtles, birds, and crocodilians). Instead, turtles have a novel abdominal-muscle-based ventilatory apparatus whose evolutionary origin remains a mystery.

Methods. Here we show through broadly comparative anatomical and histological analyses that the earliest stem-group turtle form the middle Permian(260 mya), *Eunotosaurus africanus*, has several turtle-specific lung ventilation characters: rigid ribcage, inferred loss of intercostal muscles which drive costal ventilation in all other amniotes, and histological correlates for the primary muscle, *M. transverses*, used in exhalation.

Results. Our results place the origin of the unique lung ventilatory apparatus of extant turtles shortly after the divergence of turtles from other reptiles and approximately 50 million years

before the oldest known fully developed shell.

Discussion. These data indicate that it was an easing of structural constraints through division of function (divergent specialization) between the ribs and abdominal musculature that facilitated the evolution of both the novel turtle lung ventilation mechanism and the turtle shell.

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