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Editorial: Tetrapod water-land transition: Reconstructing soft tissue anatomy and function

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Editorial on the Research Topic
Tetrapod Water-Land Transition: Reconstructing Soft Tissue Anatomy and Function

Thanks to new methods of modeling and analysis, we are discovering much more about movement, sensation, and feeding in animals that span the tetrapod water-land transition and the origin of amniotes. As investigations of function in extinct animals become more complex and rigorous, the need to take soft tissues into account becomes more pressing. For example, biomechanical simulations of locomotion in early tetrapods rely on assumptions about their muscles and cartilages that come from living animals. Thus, the drive to learn more about our ancient relatives leads us to ask new questions about the relationships between hard and soft tissues over development and evolution. How did early land vertebrates transition from aquatic to terrestrial feeding? How did muscle anatomy and development change during the transformation from fins to limbs in tetrapods and with the loss of metamorphosis in amniotes? In this Research Topic, researchers approach these questions using fossils, biomechanical models, observation of living animals, and new imaging modalities that allow us to view embryonic development and adult anatomy in unprecedented detail.

Historical perspective

Soft tissue reconstructions often are subject to scientific biases, which carry direct repercussions for scientific illustrators, educators, and children who will become the next generation of scientists. Campbell et al. A; Campbell et al. B brought together a team from diverse disciplines, ethnic and cultural backgrounds, and career stages to examine current examples of racism, Western-centrism and sexism within not only biological and anthropological works, but also in prominent natural history museums. The theme of current and historical approaches to soft tissue anatomy is further developed by Pears et al., who examined the ontogeny and morphology of the pelvic musculature in chondrichthyans using a combination of modern and historical methods. Nano-CT imaging and 3D-reconstructions were used to describe development in a growth series of elephant shark embryos, while historical descriptions from the 19th century and traditional dissection methods were used to re-describe the adult anatomy. The latter paper is a fine example of how historical data can be synthesized with new observations obtained from state-of-the-art imaging methods to advance our understanding in exciting new ways.

Locomotion with fins and limbs

Improvements in imaging techniques have allowed non-destructive analysis of increasingly small specimens, both with and without contrast, which is important when utilizing rare material from endangered species. Hirasawa et al. imaged embryos of the Australian lungfish to understand the evolution of pectoral musculature and increases in number and size of appendicular muscles across the fish-to-tetrapod transition. They hypothesized that the mesenchyme needed to develop the innervation of the pectoral limb in tetrapods is absent in fish, and that the cleithrum forms a barrier to its migration along the body wall. Thus, the gradual reduction of the cleithrum in tetrapodomorph fishes may have opened the door for increased complexity of appendicular muscles. Such increase in complexity is beautifully illustrated by the comparative dissection of the coelacanth and alligator by Mansuit and Herrel, which documents an increase in appendicular muscle mass in tetrapods and larger superficial muscles compared to sarcopterygian fishes. The combination of state-of-the-art imaging of development in extant fishes with meticulous examination of museum specimens provides much needed granularity in soft tissue evolution underlying the major locomotor shifts of the fish-to-tetrapod transition.

The parallel transition from water to land in the ontogeny of extant amphibians has prompted many researchers to use amphibians as models for early tetrapods. Molnar measured articular cartilage in various salamanders and found that, regardless of size, aquatic salamanders have much thicker cartilage caps on their limb bones than terrestrial salamanders. This finding is important because the extant phylogenetic bracket (Witmer, 1995) of stem tetrapods includes animals that vary wildly in skeletal cartilage, such as lungfish, amphibians, and amniotes. Greater accuracy in estimating soft tissue dimensions will improve biomechanical models of locomotion in stem tetrapods. Abdala et al. provided an ontogenetic perspective, co-opting geographical mapping technology to quantify changes in relative size and location of tissues over pelvic development in frogs and chickens. As frogs metamorphose from tadpoles, their girdles grow much faster than those of chickens and rotate laterally, paralleling evolutionary changes that took place during the tetrapod water-land transition.

As tetrapods became independent of bodies of water for reproduction, they developed more effective and efficient terrestrial locomotion. Zwafing et al. tested the hypothesis that stem amniotes used a more erect posture by adding muscles to an existing kinematic and dynamic model of locomotion in the Permian tetrapod *Orobates* (Nyakatura et al., 2019), a fossil close to the origin of amniotes. A semi-erect, crocodile-like posture in *Orobates* produced optimal muscle strains. However, multiple postures fell within the range of reasonable muscle strains, emphasizing the great difficulty of reconstructing behavior in extinct animals.

Cranial and feeding systems

In their study of ontogenetic changes of the aquatic food uptake mode in a newt, Natchev et al. illustrate the integration of locomotion with feeding systems. Feeding mode in younger larvae was dramatically different from pre-metamorphic larvae and adults, hinting that control of the feeding apparatus is integrated with activity of the locomotor system. These changes may be triggered by formation of functional limbs during late larval development, a finding with broad implications for the evolution and physiological integration of the locomotor and feeding systems across the water-land transition.

In addition to feeding, terrestrialization in tetrapods required many other ecological adaptations, such as air-breathing. Stem tetrapods such as *Acanthostega* relied partially on a spiracle for air-breathing. The spiracle derives from an embryonic hyomandibular pouch, which is thought to have been present as a fully formed gill in early jawed vertebrates (Gegenbaur, 1872). Gai et al. demonstrated the presence of a spiracular gill in the galeaspid *Shuyu,* the sister group to osteostracans + gnathostomes, and found that the spiracle retained a respiratory function across the fish-tetrapod transition even as the morphology of the hyomandibula (stapes) transformed into the tetrapod middle ear. Thus, this manuscript brings together exceptionally preserved fossils and new advances in phylogenetics to answer a long-standing evolutionary question. Working in another region of the skull, Clement et al. investigated the complex relationship between the brain and endocast (the cavity which houses the brain) in extant amphibians. In addition to producing detailed reconstructions of brain morphology that can be used for future interpretation of fossils, they show the importance of ecology when using an extant phylogenetic bracket, given that brain size can vary between 1 and 78% of the endocast volume.

As the amniote lineage became independent from an aquatic milieu and acquired a cleidoic egg, the larval stage was lost. Freed from the constraint of larval feeding (Werneburg, 2019), cranial bones and jaw musculature evolved new ontogenetic pathways. The most obvious changes relate to the formation and diversity of the temporal skull region, including number of temporal openings (Abel and Werneburg, 2021). In two studies presented herein, the Late Permian reptile *Captorhinus aguti* was used to represent ancestral amniotes. The complexity of skull sutures was studied to infer the degree of cranial kinesis, and weakly sutured regions of the skull were identified as potential locations for evolution of temporal openings (Abel et al.). Taking *C. aguti* as a template, Werneburg and Abel simulated temporal openings inside the anapsid skull using the Anatomical Network approach (Werneburg et al., 2019; Sookias et al., 2020). The authors show that evolution of the temporal skull region is most clearly understood in the context of feeding adaptations to hard or soft food items. Nevertheless, also other factors such as skull dimensions, neck posture, and phylogenetic constraints must be considered to permit a balanced discussion on the origin and meaning of temporal skull openings.

In this Research Topic, an exceptional group of international scientists discussed recent developments in vertebrate terrestrialization. Using modern analytical and conceptual frameworks, they defined new avenues for future research in vertebrate locomotion, feeding, and cranial anatomy. The challenges are not trivial: for animals on both sides of the water-land transition, reconstructing soft tissues based on extant relatives is difficult because of the great morphological gap between fish and tetrapods. Even in relatively conservative regions such as the braincase, factors other than phylogeny are important, such as ecology, habits, and lifestyle. In these cases, a better understanding of structure-function relationships in extant taxa can help to constrain reconstructions. In the case of evolutionary novelties such as the tetrapod limb, developmental and genetic approaches may be needed to supplement morphological comparisons. Yet, despite its difficulties, incorporating soft tissues into fossil reconstructions has many benefits, from testing and refining fossil-based locomotor hypotheses to predicting the consequences of changes in skull morphology for feeding. In addition, newly developed approaches to soft tissue reconstruction can complement historical methods and promote a more accurate, less biased understanding of evolution, whether it be in more recent or ancient human ancestors.

Author contributions

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Conflict of interest

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