How did we get four limbs? Because we have a belly

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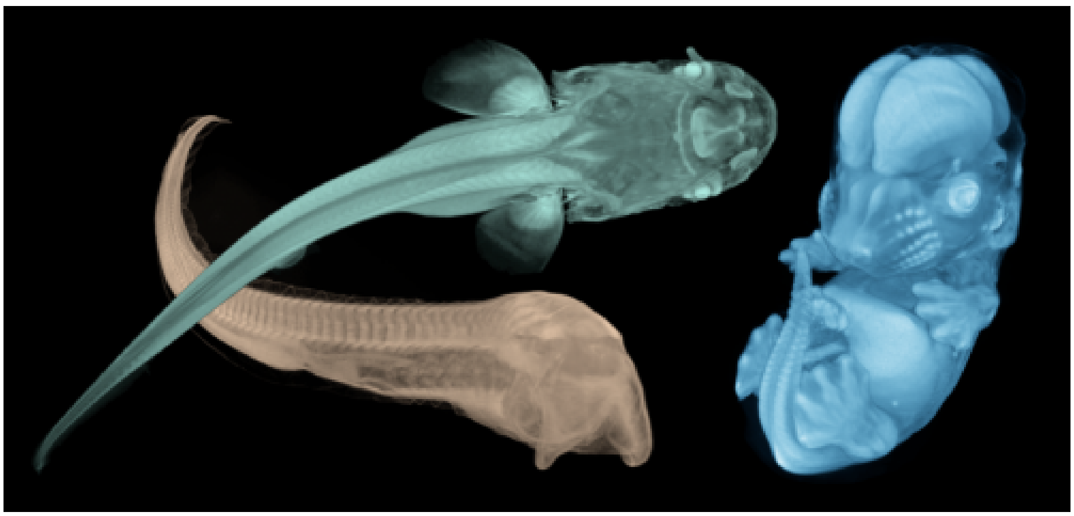

The picture shows lamprey and sturgeon hatchlings as well as a mouse embryo, all imaged with x-ray microtomography. Credit: Copyright: Brian Metscher

All of us backboned animals – at least the ones who also have jaws – have four fins or limbs, one pair in front and one pair behind. These have been modified dramatically in the course of evolution, into a marvelous variety of fins, legs, arms, flippers, and wings. But how did our earliest ancestors settle into such a consistent arrangement of two pairs of appendages? – Because we have a belly. Researchers in the Theoretical Biology Department at the University of Vienna and the Konrad Lorenz Institute for Evolution and Cognition Research have presented a new model for approaching this question in the current issue of the journal *Evolution & Development*.

As with any long-standing question in evolutionary biology, numerous ideas have been proposed to explain different aspects of the origin of paired appendages in vertebrates known as gnathostomes, which includes all living and extinct animals having both a backbone and jaw. "This group does not include the living lampreys and hagfishes, which have neither jaws nor paired fins, although they do have median fins along the midline of the back and tail", says Brian Metscher from the Department of Theoretical Biology. Any explanation must account for not only the fossil evidence, but also for the subtleties of the early development of fins and limbs.

Pairs of appendages situated at front and back ends of the body cavity

"We have drawn together a large body of molecular embryology work, as well as results from paleontology and classical morphology to work out an overall explanation of how the vertebrate embryo forms pairs of appendages along each side, and only two pairs situated at front and back ends of the body cavity," said Laura Nuño de la Rosa, lead author of the study and post-doctoral fellow at the Konrad Lorenz Institute in Altenberg, Austria.

Embryo segregates into three main layers of tissue

The proposed model incorporates results from much previous research, including information on gene expression and on interactions among the different tissues that make up an early vertebrate embryo. In its earliest stages of development, an embryo segregates into three main layers of tissue: an outer one (ectoderm) that will form the skin and nervous system, an inner layer (endoderm) that becomes the digestive tract, and an in-between layer (mesoderm) that eventually forms muscles, bones, and other organs. The early mesoderm splits into two layers that line the inside of the body cavity and the outside of the gut.

The new hypothesis proposes that fins or limbs begin to form only at the places where those two layers are sufficiently separated and interact favorably with the ectodermal tissues – namely at the two ends of the forming gut. In between, no fin/limb initiation takes place, because the two mesoderm layers maintain a narrower separation and, the authors propose, interact with the developing gut.

Behind the back end of the digestive tract (the anal opening), along the bottom of the tail, the two mesoderm layers come together as the body wall closes up, forming a single (median) fin. Along the length of the developing gut, the body wall cannot close completely, so the conditions for initiating fins or limbs occur to the left and right of the midline, allowing the development of paired instead of median fins. "You could say that the reason we have four limbs is because we have a belly," adds Laura Nuño de la Rosa.

"The most important function of a model like this is to provide a coherent framework for formulating specific hypotheses, which can be tested with molecular and other laboratory methods," says Brian Metscher, Senior Scientist in the University of Vienna's Department of Theoretical Biology. This work is also a contribution to the ongoing discussion of the roles of changes to embryonic development in the evolution of new structures, or evolutionary novelties. Further, the focus of the hypothesis on global embryonic patterning and tissue interactions emphasizes the importance of accounting for factors other than genes (epigenetics) to understand development and evolution.

More information: Laura Nuño de la Rosa, Gerd B. Müller, Brian D. Metscher: The Lateral Mesodermal Divide: An Epigenetic Model of the

Origin of Paired Fins. *Evolution & Development*, January 2014, 38-48.
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