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Elpistostege: a fish with legs or a tetrapod with fins?

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The recent discovery of a complete 375 million-year-old fossil from eastern Canada, Elpistostege watsoni, clarifies our understanding of the origin of digits and hands in tetrapods. This subject has puzzled evolutionary biologists for more than 150 years. The Devonian Elpistostege had digits embedded in its pectoral fin - a condition preceding the origin of hands in tetrapods.

Image credits: Katrina Kenny

Around 350 B.C., the Greek philosopher Aristotle asserted that our hand is the “tool of tools.” Our hands and fingers help us to work, to create, to communicate. But when did these anatomical structures appear in our distant ancestors? For the past 530 million years (Ma), certain evolutionary events have characterized the history of vertebrates. The origin of tetrapods, four-legged vertebrates, represents one of these crucial events that is associated with the water-to-land transition and the origin of fingers.

Today, tetrapods include more than 33,879 living species of amphibians, turtles, lizards, snakes, crocodilians, birds and mammals. All these tetrapods have or once had limbs rather than fins as did their fish ancestors, the lobe-finned fishes or sarcopterygians. The oldest fossilized remains of tetrapod limbs come from the end of the Devonian period (363-359 Ma ago): *Tulerpeton* from Russia and *Acanthostega* and *Ichthyostega* from Greenland. At the transition between these early tetrapods and typical lobe-finned fishes, three species of elpistostegalians best demonstrate shared intermediate morphologies. *Panderichthys rhombolepis* from the Baltic region, *Elpistostege watsoni* from Quebec, and *Tiktaalik roseae* from the Canadian Arctic.

Previous to our discovery, only three specimens of *Elpistostege* had been found: a partial skull roof, a partial three-dimensional snout and a small section

of the trunk. All this material came from the Upper Devonian Escuminac Formation (ca. 375 Ma) from eastern Canada, an exceptional fossil site recognized as UNESCO World Heritage. In 2010, a 1.57-meter-long specimen of *Elpistostege* was found at the base of the Escuminac Formation. This fossil is not only a complete specimen of *Elpistostege* but the most complete specimen of any elpistostegalian.

We analyzed this exceptional fossil using high-energy computed tomography (CT-scan). We uncovered, pixel by pixel, the anatomy of *Elpistostege*. Thousands of virtual images reveal the differential density of the fossilized bones and the rock to make it possible to visualize the fossil inside the rock, and more specifically its pectoral fins. The skeleton of *Elpistostege* pectoral fin revealed the presence of a humerus (arm), a radius and an ulna (forearm), rows of carpus (wrist) and phalanges organized in fingers. This is the first time that unequivocal fingers locked within a fin with fin rays have been discovered. This represents the most tetrapod-like arrangement of bones found in any pectoral fin.

A priori, it might seem obvious to identify what hands and fingers are. However, this evidence is less apparent when we have to define these anatomical structures in order to cover the diversity of such structures observed in tetrapods. We define the fingers as “sets of small internal bones (phalanges), of relatively uniform shape and size, which align with each other.” These phalanges form the tip of the paired appendages of vertebrates, the fingers in our arms and the toes in our legs. This definition applies to all living and fossil tetrapods, including elements found in the pectoral fin of *Elpistostege*.

When Westoll named *Elpistostege watsoni* in 1938 he described its partial skull as that of a ‘stegocephalian’, an ancient amphibian, which according to him provided "a perfect transition" between lobe-finned fish and tetrapods. In 1985, Schultze and Arsenault described the 3D partial snout and refuted the idea that *Elpistostege* was a tetrapod, instead, they suggested that it was closely related to *Panderichthys* and that these two species of fish were the closest relatives of tetrapods. Recent phylogenetic hypotheses regarding the position of *Elpistostege* suggested that *Elpistostege* and *Tiktaalik* were the tetrapod closest relatives. To determine the most likely phylogenetic position of *Elpistostege*, we analyzed 202 anatomical features in 43 species using two evolutionary approaches. The first one based on maximum parsimony and the second based on a Bayesian approach. Both methods provided the same result whereby *Elpistostege* is considered to be more derived than *Tiktaalik* and representing the sister-group of the remaining tetrapods. But where is the limit between a fish and a tetrapod?

For decades, a set of evolutionary novelties was identified to characterize tetrapods. However, there is always a possibility of discovering new fossils that may share only part of these diagnostic characters, and therefore change the definition of the Tetrapoda. Almost 20 years ago, it was suggested that tetrapods are defined as organisms derived from sarcopterygians, which first possessed fingers comparable to those of *Homo sapiens*. Therefore, since *Elpistostege* undoubtedly has fingers, rudimentary as they are, this character makes *Elpistostege* not a fish, but a primitive tetrapod. *Elpistostege* is not necessarily the ancestor of all other tetrapods, but it is the closest to what one might consider a "missing link".