Arms and legs

If you can remember dissecting the Dogfish (*Scliorhinus canicula*), you are probably nearly as old as the author. This primitive cartilagenous fish was the marker vertebrate for many of us, and seen as a more interesting prospect than the Frog (probably a size thing). This kind of dissection is now seen as a marker of an old-fashioned approach to morphology, but recently the Dogfish has sprung back into the developmental centre stage, because of surprising findings about its ‘limbs’.1

The current range of structures that can be described under the term limb had their origins in structures evident as paired fins running the entire length of the body. These can be traced to the Ordovician (463–439 million years ago, or Mya). Not until the jawed vertebrates (gnathostomes) appeared did a plan of paired pectoral and pelvic appendages become evident. This plan has not been modified since, and the development of later modifications, including digits, depended on the modification of pre-existing genetic systems. Fore-limbs and hindlimbs evolved simultaneously, and hands and feet appeared at the same time as digits; there does not appear to have ever been an animal with fingers but no toes (despite convincing accounts, there are no mermaids). The independent evolution of serially homologous appendages such as wings in bats, birds and pterosaurs, provides a striking range of phenotypes, but these structures have numerous similarities with their legs.

The linkage between fore and hind limbs apparently arose during the Palaeozoic (from 286 Mya) in these early fishes. It is probable that the *Hox* genes played a part in the process of development of paired appendages—the unpaired fins of fish develop without the expression of homeobox genes. *Hox* genes are expressed in limb buds and in the adjacent mesoderm of the trunk, and are necessary for both antero-posterior (AP) and proximo-distal patterning in the limb bud. Some differences exist in the expression of *Hox C* group genes in fore and hind limbs, but the *Hox A* and *Hox D* groups are expressed in the same way in both. However, in the forelimb, they are expressed well anterior to their pattern of expression in the trunk, and it has been suggested that distinct forelimb of tetrapods depends on the AP ‘advance’ of these genes. As there is variation among vertebrates in the number of segments that contribute to the different parts of the AP axis, the limbs of different vertebrates arise at different somite levels. However, their position with respect to *Hox* gene expression is constant. The forelimb buds are always located at the most anterior region of expression of *HoxC*-6;2 and this basic patterning mechanism is probably homologous in all organisms that share these genes.

It has been accepted for many years that the two pairs of limbs in the tetrapods evolved by subdivision of an elongated lateral fin or by restriction of the lateral paired fins to more localized structures. But, back to the Dogfish—Tanaka and colleagues found no evidence (morphological or gene expressive) for a lateral shelf running the length of the body in this primitive fish. Rather, there was clear evidence of distinct pectoral and pelvic limb bud development as semicircular flaps with well-defined apical folds, and with a clear dorso-ventral determination. The T-box transcription factors *Tbx4* and *Tbx5* appear to play a key role in specifying limb buds to form hindlimbs or forelimbs, respectively.3 The Dogfish has both, but Amphioxus has a combined version, suggesting that this fore and aft distinction arose very early in the vertebrate lineage. So study of this well-established teaching model using the methodology of modern biology has radically altered our view of early limb development.

Incidentally, why only five fingers? The earliest known Devonian tetrapods (408–360 Mya) had limbs with 6, 7 or 8 digits. This primitive polydactyly appears to have been restricted subsequently, perhaps by developmental constraints.4 A pattern of more than five digits has never been adopted as the norm, despite the existence of mutations giving rise to extra digits, and the apparent advantages that have lead to the adaptation of carpal bones into, for example, the Panda’s thumb.5 No one has anything sensible to say on this, in my view.
But I am an indifferent opinion; I quite enjoyed dissecting the Dogfish.

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References