

# The evolution of the pectoral girdle

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## ABSTRACT

The pectoral girdle articulates the forelimb with the axial skeleton in all vertebrates with paired anterior appendages. The structure of the pectoral girdle and its position along the axial skeleton has changed significantly during vertebrate evolution. These morphological changes have been well described, but there is little comparative embryology to indicate how these changes may have occurred. It is equally obscure how the muscles that connect the head with the pectoral girdle have maintained appropriate attachments even though these 2 structures have become separated. Here I review the changes in the pectoral girdle across different vertebrate taxa, indicating, where known, the developmental mechanisms underlying these changes. I also suggest how the muscular connections between the head and pectoral girdle have been maintained between these once adjacent bones, displaced during vertebrate evolution.

*Key words:* Pectoral girdle; evolution; neural crest; vertebrate.

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## INTRODUCTION

The pectoral girdle is present in all extent vertebrates that possess paired anterior appendages and is a complex structure, consisting of both endochondral and dermally derived skeletal elements. This structure forms an incomplete circle of paired skeletal elements around the axial skeleton that acts as a brace for the forces exerted by locomotion while allowing maximum flexibility of limb movement. These forces and the ranges in flexibility vary quite considerably between aquatic and terrestrial dwelling vertebrates and as a consequence, the pectoral girdle is a structure that exhibits great variation between different vertebrate taxa (Fig. 1).

The problems of how and why the position of the paired forelimbs changed along the body axis during vertebrate evolution have puzzled developmental and evolutionary biologists for many years. Equally puzzling but less studied is how the skeletal elements of the pectoral girdle, many of which are derived from territory outside of the developing limb field, are positioned in order to connect the forelimb to the axial skeleton. However there is a shortage of comparative embryological data to suggest how these changes occur.

## THE ORIGIN OF THE PECTORAL GIRDLE

In the fossil record, the first appearance of paired fins occurred in anaspids, members of the agnathan group of fishes. However, in these fossils, there is no evidence of articulation with the axial skeleton (Janvier, 1996; Coates & Cohn, 1998). The most ancient fossils to have pectoral fins with a primitive internal skeleton are the agnathan osteostracans. They also exhibit a point for the endochondral limb skeleton to articulate with the head shield (Fig. 2A) (Coates, 1994). The head shield of agnathans consists of dermal plates that cover the head and it is likely that a portion of the pectoral girdle evolved from this structure. The cranial position of the forefin and cranial integration of the pectoral girdle led to some of the earliest theorists on limb/girdle evolution proposing that the pectoral girdle had evolved from a modified gill arch (see Zangerl, 1981), an implication of this being that the pectoral girdle was a neural crest derivative. However, this theory has largely been replaced by the fin fold theory (see Coates, 1994) and furthermore, experimental embryology has also shown that the pectoral girdle is derived exclusively from the mesoderm (Chevallier, 1977; Burke, 1991; Huang et al. 2000).

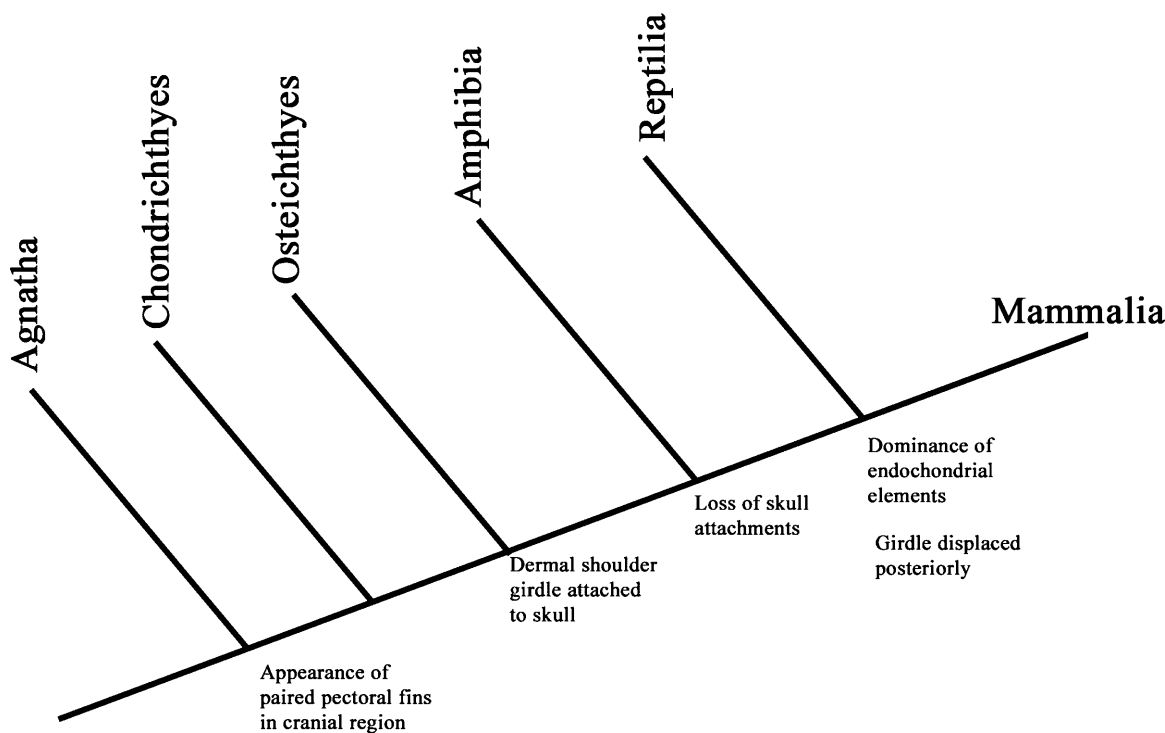


Fig. 1. Phylogenetic relationship of the vertebrates, indicating key changes in the pectoral girdle between taxa.

#### MOVEMENT OF THE LIMB FIELD ALONG THE BODY AXIS

It is clear from both extant and extinct vertebrates that there have been significant changes in the positioning of the forelimbs and pectoral girdle since their appearance in agnathan fish. However, until recently, there was no indication of the developmental mechanisms that underlie these changes.

In the jawed fish such as osteichthyes (bony fish, Fig. 2*B*) and chondrichthyes (cartilaginous fish, Fig. 2*C*), the pectoral girdle is positioned at the base of the skull, encircling the anterior-most trunk vertebrae. In amphibia, however, there appeared the first change in the relationship between the pectoral girdle and the head (Fig. 2*D*). The first trunk vertebra underwent modification to allow articulation with the skull. This new type of vertebra, called cervical, was inserted between the pectoral girdle and the skull (Torrey, 1978), displacing the pectoral girdle posteriorly. In the reptile lineage, there was a further modification of vertebrae into 5 distinct types, accompanied by massive variation in the numbers of cervical vertebrae present, a phenomenon known as transposition (Goodrich, 1906). The extremes of this variation are exemplified by the fossil diapsid *Muraenosaurus* which had 76 cervical vertebrae (Young, 1981) and the snake which does not have any. Between reptiles with forelimbs there is also an apparent variation in the

positioning of the limb and pectoral girdle in relation to the head. However, this is due to variation in length of cervical territory, as the limb and pectoral girdle are always positioned lateral to the transition between the cervical and thoracic vertebrae (Fig. 2*E*). In contrast to the massive variation seen in the reptile lineage, mammals have a fixed number of 7 cervical vertebrae (Fig. 2*F*), and variation in the length of the cervical region is brought about by differences in size of the vertebrae. Again, however, compared to the axial skeleton, the pectoral girdle is positioned at the cervical/thoracic boundary.

The anamniote pectoral girdle is formed from lateral plate mesoderm while the amniote has an additional somitic component (Chevallier et al. 1977; Burke, 1991). It has been shown experimentally that in relation to the axial skeleton, this mesoderm originates from a large region of both cervical and thoracic territories in the developing chick embryo (Kieny et al. 1972; Chevallier et al. 1977; Huang et al. 2000). What is not clear is how this tissue moves and is positioned in relation to the developing axial skeleton and the limb. It is tempting to think that signals dictating the cervical/thoracic transition in the axial skeleton, such as the *Hox6* gene (Burke et al. 1995) may also play a role in dictating the position of the pectoral girdle along the axis. However, *Hoxb5* knockout mice would suggest otherwise. In this mutant there is anteriorisation of the vertebrae at the

cervical/thoracic boundary, but instead of posterior displacement of the scapula and limb there is anterior displacement (Rancourt et al. 1995). This would suggest that positioning of the limb and shoulder girdle are actually independent of the axis. This has been proved to be correct in positioning of the chick limb where it is expression of Hox 9 paralogues in the lateral plate mesoderm that dictate the position along the axis (Cohn et al. 1997). Thus it is likely that Hox genes expressed in the lateral plate are also responsible for positioning at least the endochondral shoulder girdle in amniotes. It will be interesting to see if the same molecular mechanisms position the dermal elements, seen in greater abundance in anamniotes (see below).

#### CHANGES IN THE COMPOSITION OF THE PECTORAL GIRDLE DURING VERTEBRATE EVOLUTION

Along with variation in the positioning of the forelimbs and pectoral girdle along the axis during vertebrate evolution, there have also been significant changes in the individual skeletal elements that make up the pectoral girdle. There are abundant theories as to the evolutionary pressures that drove these changes, but scant developmental data to indicate how these changes were made.

Paired fins first appeared in the vertebrate lineage in agnathan (jawless) fish and would have conferred stability rather than propulsion. Fossils show a skeletal element, thought to be an expanded endochondral basal fin element (Fig. 2A) (Jarvik, 1980) articulated with the dermal head shield. However, the homology between individual dermal plates and the individual elements of the pectoral girdle in later vertebrates is not clear.

Osteichthyes consist of 2 groups, the actinopterygians and the sarcopterygians (including the crossopterygians). The pectoral girdle in this group has been well described and sits at the posterior edge of the gill chamber. It generally consists of a small endochondral bone—the scapulocoracoid with an articulation point for the fin, called the glenoid fossa. This is embedded in a group of large dermal bones. These consist dorsally of the posttemporal and postcleithrum, which attach the girdle to the skull. More ventrally, the largest element, the cleithrum (into which the scapulocoracoid is embedded) attaches to the clavicle, the ventral-most structure (Fig. 2B). There is however some variation in this pattern in both extinct and extant osteichthyes, and additional dermal bones can be found in some groups, whilst in

others dermal elements have been lost (Kardong, 1998). In the crossopterygians there was the addition of a single (as opposed to paired) element in the ventral pectoral girdle—the interclavicle, which is thought to have formed from an enlarged dermal scale (Kardong, 1998). This transition to well defined, robust dermal girdle is a reflection of the more active, predatory existence of jawed fish, requiring increased stability and control provided by muscularised fins. However, the developmental changes involved in this transition are unknown as no extant agnathan possesses paired fins.

Chondrichthyes, as the name suggests, possess only cartilagenous skeletal elements and as a consequence the pectoral girdle is radically reduced. In more primitive members, it consists of a paired cartilaginous element. In more modern groups this has become fused across the dorsal midline to become the scapulocoracoid bar (Fig. 2C) (Kardong, 1998).

Amphibia represent the first tetrapods. The vastly different forces required for movement on land brought about considerable changes in the composition of the skeletal elements in the pectoral girdle. The dermal armour elements sunk inwards, integrating with the endochondral elements, to become a brace to transmit the force of movement to the axial skeleton. Consequently, they also became bigger and more robust to fulfil this role. The most dramatic change in composition of the amphibian pectoral girdle was loss of the bones that connected the girdle to the skull (Fig. 2D). This consequently allowed the head to become more mobile and allowed independent movement between the head and the limbs, an obvious advantage for terrestrial dwelling. This pattern changed further in different groups of more modern amphibians with the cleithrum absent in almost all groups. Anurans (frogs and toads) are the only extant vertebrates to retain the cleithrum (Young, 1981).

The main changes in the reptilian pectoral girdle occurred in the endochondral elements, which became larger and more prominent than the dermal elements. In addition to the existing lateral plate mesoderm component, the amniote scapula acquired a somite-derived portion, which forms the shoulder blade in the chick (Chevallier, 1977; Huang et al. 2000) and may explain the increased size of this element. It has been shown in both chick and mouse embryos that the scapula head (derived from lateral plate mesoderm) requires the expression of Pax-1 for its development (Timmons et al. 1994; Dietrich & Gruss 1995; Hofmann et al. 1998; Wilm et al. 1998), while the other lateral plate derived elements do not. However, comparative data are not available from anamniotes.

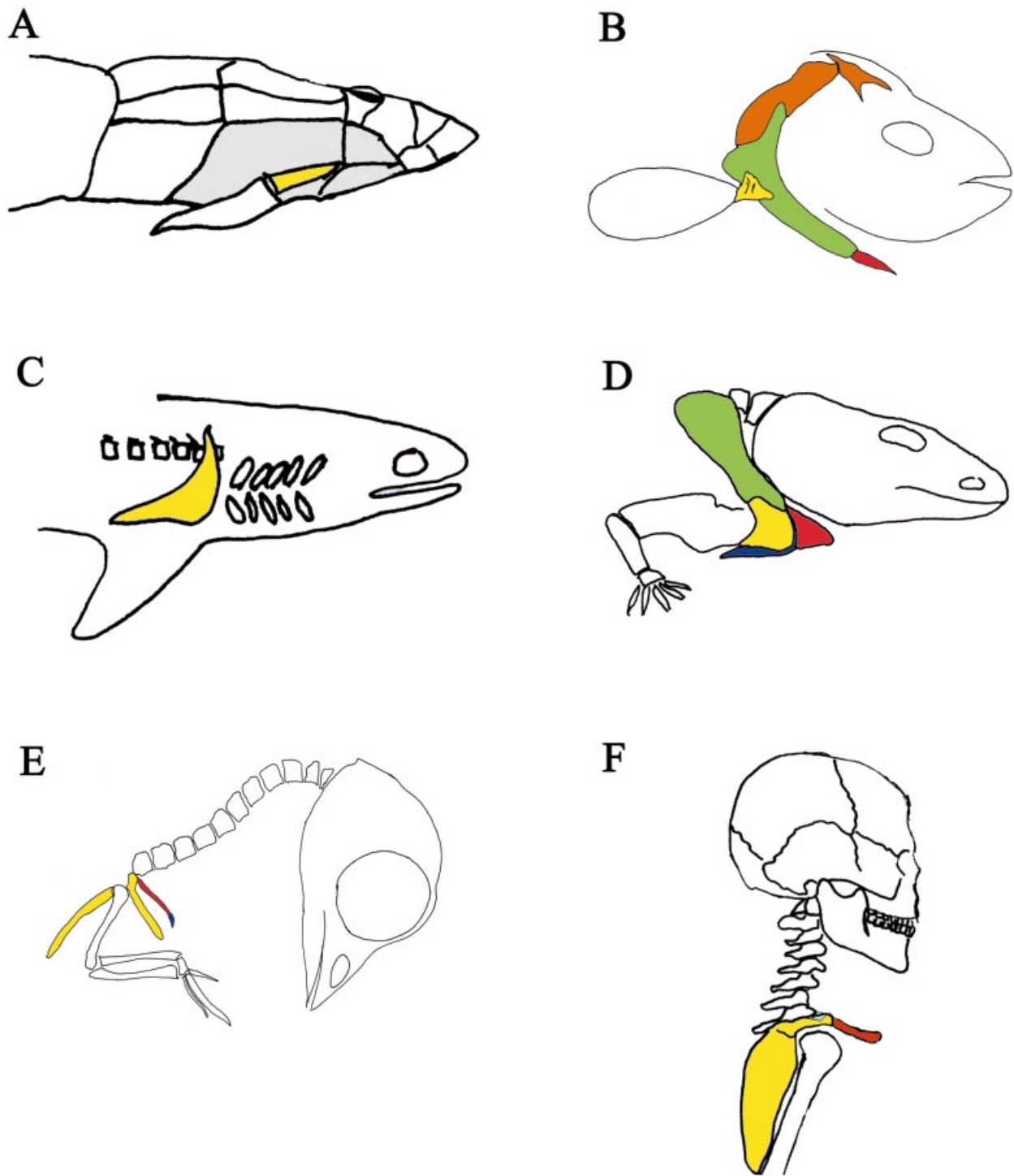


Fig. 2. (A) Extinct agnatha: bony dermal plates cover the head. Spinelike pectoral fin is connected to the head shield by an expanded endochondral basal fin element. Area shaded grey is prospective dermal shoulder girdle, but homology to individual girdle elements seen in later vertebrates is not certain. (B) Osteichthyes: dermal shoulder girdle is well developed and connected to the skull dorsally. Endochondral scapulocoracoid is small by comparison. (C) Chondrichthyes: shoulder girdle consists only of single scapulocoracoid element, positioned cranially. (D) Primitive amphibian: dorsal elements connecting the girdle to the head have been lost. The girdle is still dominated by dermal elements and is positioned just behind the new first cervical vertebra. (E) Reptile: chicken. Major dermal elements have been lost and the scapula and procoracoid bones are now separate. Cervical expansion has displaced the girdle and limb posteriorly. (F) Mammal: human. The endochondral scapula dominates the girdle. The coracoid process has fused to the scapula. The girdle is positioned lateral to the cervical/thoracic boundary in the axial skeleton. Key: Orange, posttemporal and postcleithra; green, cleithra; red, clavicle; yellow, scapulocoracoid or scapula and procoracoid; dark blue, interclavicle; light blue, coracoid process.

In most reptiles 2 separate endochondral condensations form, reflecting the fact that the scapula and procoracoid have become separate structures (Torrey, 1978) (Fig. 2E). In some synapsid reptiles, the reptile group that led to mammals, there are 2 coracoid condensations in addition to the scapula (Kardong, 1998). The procoracoid is homologous to the fish/amphibian element while the second (posterior) newer coracoid is homologous with the mammalian coracoid. However, it has recently been suggested that birds (diapsids) also possess this newer coracoid condensation (Huang et al. 2000). Of the dermal elements, only the ventral-most clavicles and interclavicles persist and these tend to become smaller.

Monotremes, the most primitive mammals, have a very reptile-like pectoral girdle (Young, 1981). However, this pattern is significantly changed in therian mammals. Marsupials lose the interclavicle, the procoracoid disappears and the coracoid becomes significantly reduced in size. Eutherian (placental) mammals also lose the interclavicle and the clavicle is generally much smaller. In some instances, such as in ungulates, the clavicle is lost, leaving the girdle without any dermal contribution. This progressive loss of ventral elements is related to a change in stance. Amphibians and reptiles have laterally positioned limbs that require ventral bracing. Mammalian limbs are held directly beneath the body and require lateral bracing from the scapula. Thus the mammalian pectoral girdle is dominated by the scapula, which becomes the articulation point with the limb (Young, 1981; Kardong, 1998). It has been shown in mice that, in addition to Pax-1, Hoxa-5 and PDGF $\alpha$ R are necessary for correct development of this articulation point, the scapula head (Jeannotte et al. 1993; Soriano, 1997). The coracoid becomes much reduced and completely fused to the scapula to form the coracoid process (Fig. 2F).

#### MAINTENANCE OF MUSCULAR CONNECTIONS BETWEEN THE HEAD AND THE PECTORAL GIRDLE

Although there is great variation in the positioning and composition of the pectoral girdle in vertebrates, one conserved feature is the connection between the head and the girdle by groups of muscles. Ventrally, these muscles connect the tongue skeleton to the clavicle and have the important function of stabilising the larynx during the swallowing of food, preventing it from being inhaled. However, it has not been understood how these muscles connect correctly

between skeletal elements that are no longer in close apposition. In the head, cranial neural crest cells form connective tissue fascia that anchor the origin and insertion points of muscles to skeletal elements (Noden, 1983). They maintain skeletomuscular connectivity by anchoring exclusively to skeletal elements derived from exactly the same crest population that they are derived from themselves. If one end of the muscle inserts into a mesodermally derived bone in the skull, a discrete cluster of cranial neural crest cells is found in the bone at the insertion point, maintaining this patterning system (Kontges & Lumsden, 1996). We have found that this is also true for muscles that connect the tongue skeleton and the mesodermally derived clavicle in the chick embryo, through a population of cranial neural crest cells that migrate into the trunk (I. M. McGonnell, I. McKay and A. Graham, unpublished observations).

Thus there has been a progressive posterior displacement of the pectoral girdle and the limb away from the head during the evolution of the vertebrates, probably due to the expansion of the cervical territory and the formation of the neck. However the same mechanisms that are employed in the head to maintain skeletomuscular connectivity are still employed to ensure muscular connection between the head and the pectoral girdle.

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