

# Reconstructing pectoral appendicular muscle anatomy in fossil fish and tetrapods over the fins-to-limbs transition

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## ABSTRACT

The question of how tetrapod limbs evolved from fins is one of the great puzzles of evolutionary biology. While palaeontologists, developmental biologists, and geneticists have made great strides in explaining the origin and early evolution of limb skeletal structures, that of the muscles remains largely unknown. The main reason is the lack of consensus about appendicular muscle homology between the closest living relatives of early tetrapods: lobe-finned fish and crown tetrapods. In the light of a recent study of these homologies, we re-examined osteological correlates of muscle attachment in the pectoral girdle, humerus, radius, and ulna of early tetrapods and their close relatives. Twenty-nine extinct and six extant sarcopterygians were included in a meta-analysis using information from the literature and from original specimens, when possible. We analysed these osteological correlates using parsimony-based character optimization in order to reconstruct muscle anatomy in ancestral lobe-finned fish, tetrapodomorph fish, stem tetrapods, and crown tetrapods. Our synthesis revealed that many tetrapod shoulder muscles probably were already present in tetrapodomorph fish, while most of the more-distal appendicular muscles either arose later from largely undifferentiated dorsal and ventral muscle masses or did not leave clear correlates of attachment in these taxa. Based on this review and meta-analysis, we postulate a stepwise sequence of specific appendicular muscle acquisitions, splits, and fusions that led from the ancestral sarcopterygian pectoral fin to the ancestral tetrapod forelimb. This sequence largely agrees with previous hypotheses based on palaeontological and comparative work, but it is much more comprehensive in terms of both muscles and taxa. Combined with existing information about the skeletal system, our new synthesis helps to illuminate the genetic, developmental, morphological, functional, and ecological changes that were key components of the fins-to-limbs transition.

*Key words:* Sarcopterygii, stem tetrapods, water-land transition, extant phylogenetic bracket, *Eusthenopteron*, *Acanthostega*, *Pederpes*, Tetrapoda.

## CONTENTS

I. Introduction .....	2
II. Muscle homology and osteological correlates in extant lobed-finned fish and tetrapods .....	4
(1) Musculoskeletal anatomy of the pectoral fins of extant sarcopterygian fish .....	5
(a) Extant coelacanth .....	6
(b) Extant lungfish .....	7
(2) Musculoskeletal anatomy of the pectoral limbs of extant tetrapods .....	9
(a) Salamanders (Urodela) .....	10
(b) Lizards (Squamata) .....	11

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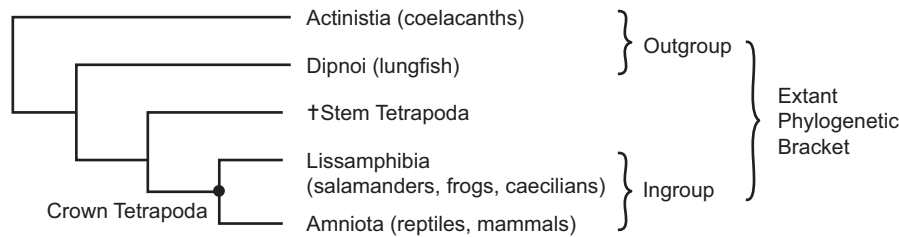
III. Review of osteological correlates in fossil sarcopterygians .....	12
(1) Pectoral girdle .....	12
(a) Onychodontids and dipnomorphs .....	12
(b) Tetrapodomorph fish .....	12
(c) Stem tetrapods .....	13
(d) Crown tetrapods .....	15
(2) Humerus .....	15
(a) Onychodontids and dipnomorphs .....	15
(b) Tetrapodomorph fish .....	16
(c) Stem tetrapods .....	18
(d) Crown tetrapods .....	19
(3) Radius/ulna .....	19
(a) Onychodontids and dipnomorphs .....	19
(b) Tetrapodomorph fish .....	19
(c) Stem tetrapods .....	20
(d) Crown tetrapods .....	21
IV. Proposed homologous osteological correlates in the sarcopterygian lineage: from fish to tetrapods .....	21
(1) Pectoral girdle .....	21
(2) Humerus .....	22
(3) Ulna .....	22
V. Reconstruction of pectoral appendicular muscles in the LCA of tetrapodomorpha, tetrapoda, and crown tetrapods .....	23
VI. Conclusions .....	28
VII. Acknowledgements .....	29
VIII. References .....	29
IX. Supporting Information .....	31

## I. INTRODUCTION

The fins-to-limbs and water–land transition in tetrapods involved interdependent changes in anatomy, behaviour, and habitat. Recent years have seen great strides in understanding the phylogeny (e.g. 2007; Ruta, 2011; Carroll, 2012; Sookias, Böhmer & Clack, 2014; Bernardi *et al.*, 2016; Clack *et al.*, 2016; Ruta & Wills, 2016; Pardo *et al.*, 2017) and palaeoecology (e.g. Clack, 2007, 2009; Retallack, Hunt & White, 2009; Clack *et al.*, 2016; Sanchez *et al.*, 2016) of stem tetrapods. The fossil evidence suggests that limbs with digits first appeared during the Late Devonian period [~385 million years ago (MYA)] in aquatic animals that probably lived in shallow, nearshore marine or brackish environments (Coates & Clack, 1995; Clack, 2007). However, recently discovered trackways place the minimum date for the origin of tetrapods (i.e. having limbs with digits) around 392 MYA, likely in an ocean lagoon environment (Niedzwiedzki *et al.*, 2010; Narkiewicz & Narkiewicz, 2015). In the context of low preservation rates and a mismatch between body fossils and trackways, hypotheses about the specific time period or environment in which tetrapod limbs first appeared should be viewed with caution (Friedman & Brazeau, 2011). It is hypothesized that the first limbs helped their owners to push through vegetation, walk underwater, or dig underwater burrows (Coates & Clack, 1995). Later, limbs were ‘exapted’ for terrestrial locomotion. But how did limbs change from the paddle-like structures of Devonian tetrapods to the robust, muscular appendages

that allow modern terrestrial tetrapods to move swiftly over varied terrain? And from what ancestral musculoskeletal configuration did the great diversity of modern tetrapod limb anatomy originate? These questions are important not only for understanding the palaeobiology of extinct tetrapods and the evolutionary and developmental biology of extant taxa, but also for understanding how animals adapt to novel environments.

The sequence of character transformations in the pectoral appendicular skeleton that accompanied the fins-to-limbs and water-to-land transitions in tetrapods has been described in detail (e.g. Coates, Jeffery & Ruta, 2002; Shubin, Daeschler & Coates, 2004; Shubin, Daeschler & Jenkins, 2006; Hall, 2008; Boisvert, 2009; Callier, Clack & Ahlberg, 2009; Ahlberg, 2011; Pierce, Clack & Hutchinson, 2012). Changes between tetrapodomorph fish such as *Eusthenopteron* and Devonian tetrapods such as *Acanthostega* include the following: in the shoulder girdle, dermal bones spanning the head–trunk boundary were lost and the endoskeletal girdle was enlarged (Coates *et al.*, 2002; Daeschler, Shubin, & Jenkins, 2006), and the orientation of the shoulder joint (glenoid) changed from posterior to posterolateral. The humerus transformed from conical, ovoid or pear-shaped to an angular, L-shaped element (e.g. Andrews & Westoll, 1970a; Boisvert, 2009), and the shape of the humeral head changed from circular to strap-like (Shubin *et al.*, 2004). The radius and ulna transformed from flattened, diverging elements of unequal length to two parallel cylinders articulating distally with multiple carpal bones (Andrews & Westoll, 1970a; Ahlberg, 2011). The distal appendicular



**Fig. 1.** Extant phylogenetic bracket of stem tetrapods. † indicates extinct clade.

skeleton lost its dermal fin rays (lepidotrichia) and gained digits. Functionally, these changes led to the pectoral limb becoming a weight-bearing appendage directed laterally rather than posteriorly (Boisvert, Mark-Kurik & Ahlberg, 2008) with restricted shoulder rotation (Shubin *et al.*, 2004; Pierce *et al.*, 2012; Pierce, Hutchinson, & Clack, 2013), and a flexed elbow (Ahlberg, 2011).

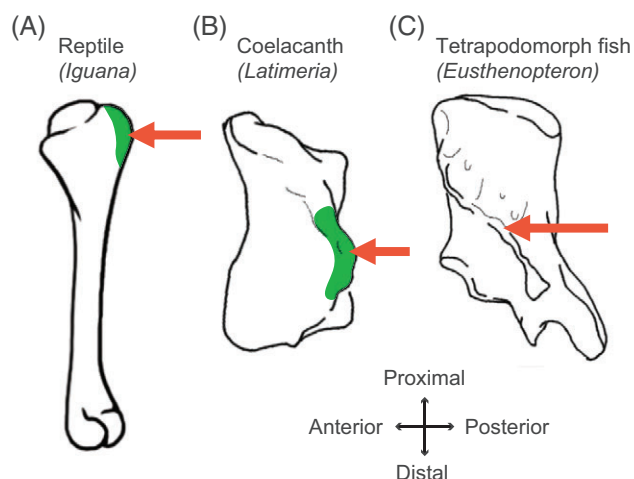
Reconstructions of soft tissue anatomy are equally important as those of the skeleton because they can provide crucial information about locomotion, mode of life, and ecology of extinct animals (Witmer, 1995). For example, muscle reconstructions have been used to infer characteristics such as posture, maximum speed, and even possible gaits in extinct vertebrates (Russell, 1972; Sumida, 1989; Hutchinson & Garcia, 2002; Sellers *et al.*, 2004, 2009; Hutchinson *et al.*, 2005; Sellers & Manning, 2007; Bates *et al.*, 2010; Schachner, Manning & Dodson, 2011). In addition, the ancestral configuration of the limbs is critical for understanding how constraints and adaptations led to the morphological diversity of modern tetrapod limbs. The transformation of fins to limbs was one of the most important events in vertebrate history, and the musculature of the earliest limbs is of fundamental importance in interpreting the changes that led to the specialized limb musculature of modern amniotes and amphibians (Miner, 1925). Furthermore, the relationships of soft tissues to osteological correlates can help to resolve phylogenetic relationships by indicating which skeletal characters are independent of each other (Witmer, 1995). For example, two skeletal features associated with the origin and insertion of the same muscle cannot be considered independent characters in a phylogenetic sense.

Previous studies have attempted to reconstruct muscle anatomy in early tetrapods and their relatives. In the early 20th century, A. S. Romer reconstructed appendicular muscle anatomy in early-diverging synapsids (Romer, 1922) and the pectoral limbs of *Diadectes* and *Eogyrinus* (Romer, 1924) based on detailed studies of modern taxa. Other notable examples of reconstruction of appendicular muscles include the fossil lungfish *Glyptolepis* (Ahlberg, 1989), the tetrapodomorph fish *Eusthenopteron* (Andrews & Westoll, 1970a), the stem tetrapod (i.e. more closely related to extant tetrapods than extant lungfish, but not part of the crown group) *Ossinodus* (Bishop, 2014), the early temnospondyl amphibian *Eryops* (Miner, 1925), and various stem amniotes (e.g. captorhinids) (Holmes, 1977; Sumida, 1989). However, these studies were not able fully to exploit information from

extant taxa because of the lack of established homologies between muscles of non-tetrapod vertebrates and tetrapods.

The most rigorous method for reconstructing soft tissues in fossils, extant phylogenetic bracketing (EPB; Witmer, 1995), is a form of phylogenetic inference (Bryant & Russell, 1992) that uses anatomical data from extant taxa, grounded in the relationship between soft tissues and their osteological correlates. In fossils, given the lack of soft tissues, established osteological correlates can stand as proxies for their corresponding soft-tissue attachments. At a minimum, the method requires identification of homologous soft tissues in an extant taxon within a clade that includes the extinct taxon of interest and in an outgroup taxon. Therefore, using EPB for stem-tetrapod limb muscles requires establishment of muscle homology between extant tetrapods (ingroup) and extant sarcopterygian fish (lungfish and coelacanths; outgroup) (Fig. 1). If a series of extant and extinct taxa along a phylogeny are studied in this way, then evolutionary sequences of changes in character states of soft and bony tissues can be reconstructed (e.g. Hutchinson, 2001).

Diogo *et al.* (2016) recently re-examined the muscle anatomy of the lungfish *Neoceratodus* (one of the only three extant genera of dipnoans) and the coelacanth *Latimeria* (the only extant coelacanth genus) and undertook a detailed comparison with other living fishes and with tetrapods in order to investigate the homology of appendicular muscles across these taxa. Their observations and comparisons indicated that many appendicular muscles present in extant dipnoans and coelacanths are homologous with muscles or muscle groups in tetrapods. Here, we re-examined the fossil literature in light of the new information and homology hypotheses provided by Diogo *et al.* (2016) in order to reconstruct pectoral appendicular muscle anatomy in ancestral sarcopterygian fish, tetrapodomorph fish, stem tetrapods, and crown tetrapods *via* EPB. First, we compiled records of osteological correlates of muscle attachment in sarcopterygian fish, including extant lungfish and coelacanths, and tetrapods, including extant lizards and salamanders, as well as various groups of extinct sarcopterygian fish and tetrapods, both from the literature and through direct examination of specimens. A summary of this information is provided in Sections II and III. Next, using the muscle homology hypotheses from the literature, we constructed a data matrix with character states for the osteological correlates of homologous muscles in each taxon. For example, the insertion of the *pectoralis* in *Sphenodon* and *Iguana* is the deltopectoral crest of the humerus (Osawa,



**Fig. 2.** Ventral view of the right humerus of bracket taxa (*Iguana* and *Latimeria*) and a fossil taxon (*Eusthenopteron*) showing identification of homologous osteological correlates (orange arrows). Green areas indicate the attachments of muscles in extant taxa that are thought to be homologous (see Table 2). The hypothesis of homology is tested by examining fossils of extinct members of each lineage. For example, *Eusthenopteron* is an extinct fish closely related to tetrapods, and it has a ridge on the ventral humerus similar to the processes from which the hypothetically homologous muscles originate in the two extant taxa.

1898) (Fig. 2A), and the insertion of the homologous muscle in *Latimeria* (a portion of the *abductor superficialis*; Diogo *et al.*, 2016) is the ventral process of the humerus ('crochet du bord inferior' *sensu* Millot & Anthony, 1958) (Fig. 2B). Third, we analysed the distribution of these correlates in fossil sarcopterygians (e.g. Fig. 2C) based on phylogenetic relationships taken from the literature, using both parsimony and likelihood analyses to reconstruct the most likely ancestral states for each character (see Section V for detailed methods). Based on this review and meta-analysis, we postulate a stepwise sequence of specific muscle acquisitions, splits, and fusions that led from the sarcopterygian pectoral fin to the ancestral tetrapod forelimb, and specify which aspects of this major morphological transition remain unclear.

Our analysis shows how integration of detailed skeletal information from fossil taxa and musculoskeletal data from extant taxa, using explicit phylogenetic methods, can provide crucial information on morphological evolution, including major anatomical innovations such as tetrapod limbs. The new perspective offered by this multidisciplinary review will provide a useful context for interpreting new fossil discoveries, and the hypotheses it generates will lay a foundation for future studies on the evolutionary transition from fish to tetrapods and from fins to limbs. For example, the study provides an anatomical 'map' for identifying potential muscle attachment sites in fossils that do not leave osteological correlates using methods such as microhistology (e.g. Sanchez *et al.*, 2013). The sequence of muscle differentiation proposed here can be tested by the results of future studies, as well as fossil discoveries that display transitional morphologies.

These hypotheses will also assist in tracking ontogenetic changes in fossil taxa; i.e. whether the presence or relative locations of certain scars or processes are associated with the ontogenetic age of a specimen (e.g. Callier *et al.*, 2009). Finally, these results provide a more rigorous framework for muscle reconstructions that will be useful for functional analyses of the appendages of fossils on both sides of the fins-to-limbs transition.

## II. MUSCLE HOMOLOGY AND OSTEOLOGICAL CORRELATES IN EXTANT LOBED-FINNED FISH AND TETRAPODS

We now briefly review the pectoral appendicular muscles of four key extant taxa – *Neoceratodus forsteri*, *Latimeria chalumnae*, *Salamandra salamandra*, and *Iguana iguana* – and hypotheses of homology between them, and describe osteological correlates of muscle attachment. *Salamandra salamandra* and *Iguana iguana* represent lissamphibians and squamates, respectively; differences from *Ambystoma mexicanum* and *Sphenodon punctatus* will be discussed. For this study we dissected specimens of *S. punctatus*, *I. iguana*, and *S. salamandra*, and we previously dissected specimens of *N. forsteri*, *L. chalumnae*, and *A. mexicanum* (Diogo *et al.*, 2016) (Table 1).

The skeletal elements of the pectoral girdle and proximal appendage (stylopod and zeugopod) in fish and tetrapods are shown in Fig. 3. Homology of the pectoral girdle, humerus, radius, and ulna among sarcopterygians is well established (e.g. Coates & Ruta, 2008). Fossil and developmental evidence indicates that the glenoid, scapular, and coracoid regions of the girdle are homologous between fish and tetrapods (Johanson, Joss & Wood, 2004). Specifically, Johanson *et al.* (2004) propose that the anterior process (coracoid) and dorsal process of the scapulocoracoid in *Neoceratodus* are homologous with the anterior and dorsal (i.e. infraglenoid and supraglenoid) 'bustresses' in fossil sarcopterygians, and with the coracoid and scapula in tetrapods, respectively (Fig. 4).

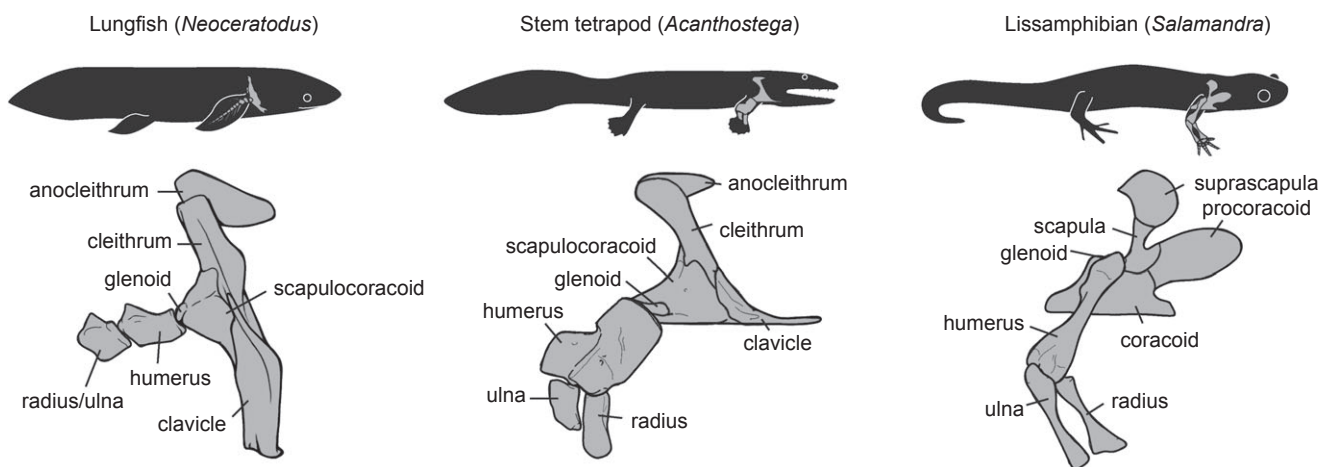
Older studies (e.g. Romer, 1922) homologized the dorsal and ventral muscle masses of fish and tetrapods, but not individual muscles. The dorsal ('dorsomesial') pectoral musculature in both fish and plesiomorphic tetrapods (i.e. lizards and salamanders) originates from the scapular region ('supraglenoid buttress') and dorsal internal surface of the pectoral girdle, while the ventral ('ventrolateral') musculature originates from the coracoid plate and posterior ventral edge of the dermal girdle (cleithrum, clavicle, and/or interclavicle; Fig. 3) (Romer, 1924). Diogo *et al.* (2009) and Diogo & Abdala (2010) likewise concluded that sarcopterygians plesiomorphically had mainly undivided dorsal ('adductor') and ventral ('abductor') muscle masses from which all the intrinsic appendicular muscles of tetrapods were derived.

More recently, studies have ventured detailed muscle homology hypotheses between extant sarcopterygian fish and tetrapods. Boisvert, Joss & Ahlberg (2013) drew homologies between individual pelvic appendicular muscles



Table 1. Extant taxa and specimens included in this study. Institutional abbreviations: Universität Tübingen (EKUT), Macquarie University (MQU), The Natural History Museum, London (BMNH), The Royal Veterinary College (RVC), Museum of Comparative Zoology, Harvard (MCZ), Howard University (HU). Specimens listed were examined by J.L.M., J.R.H, R.D and/or S.E.P.

Extant taxa			
Species	Clade	Specimen(s) examined	References
<i>Latimeria chalumnae</i>	Coelacantha	EKUT CCC162.11, CCC161	Millot & Anthony (1958), Nulens, Scott, & Herbin (2011), Diogo <i>et al.</i> (2016) and Miyake <i>et al.</i> (2016)
<i>Neoceratodus forsteri</i>	Dipnoi	MQU JVM-I-1051NC, JVM-I-1052NC	Braus (1900) and Diogo <i>et al.</i> (2016)
<i>Salamandra salamandra</i>	Lissamphibia	RVC JRH-SAL1 through SAL5	Francis (1934)
<i>Ambystoma mexicanum</i>	Lissamphibia	HU AM1, HU AM2	Diogo & Tanaka (2012, 2014)
<i>Sphenodon punctatus</i>	Rhynchocephalia	BMNH 1969.2204, BMNH 1935.12.6.1, S1/MEHJ#1, UMZC R2604	Osawa (1898), Byerly (1925), Miner (1925) and Russell & Bauer (2008)
<i>Iguana iguana</i>	Squamata	Three unnumbered specimens	Russell & Bauer (2008) and references therein



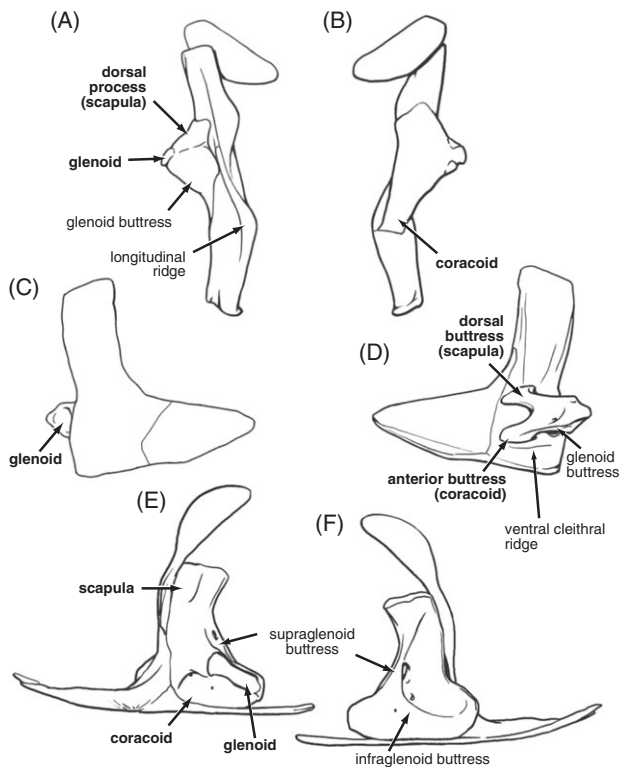
**Fig. 3.** Schematic diagram of pectoral girdle and proximal appendicular bones in a representative extant sarcopterygian fish (*Neoceratodus*; modified from Rosen *et al.*, 1981), stem tetrapod (*Acanthostega*; modified from Coates, 1996) and extant tetrapod (*Salamandra*; modified from Miner, 1925) in right lateral view. In *Neoceratodus*, the fin is shown internally rotated from neutral position so that the dorsal fin surface faces laterally and the preaxial fin edge faces ventrally in order to facilitate comparison with tetrapods.

in *Neoceratodus*, *Latimeria*, and *Ambystoma* based on comparative anatomy and development and using the data provided by Millot & Anthony (1958) for *Latimeria*. Diogo *et al.* (2016) included a new analysis of fin muscles in *Latimeria* based on dissections and computerized tomography (CT) scans (see also Miyake *et al.*, 2016), and compared the resulting data with similar data from *Neoceratodus* and *Ambystoma*. The study proposed homology hypotheses based upon: (i) embryonic primordia and sequence of development [from *Neoceratodus* and *Ambystoma* (Boisvert *et al.*, 2013); from *Ambystoma* (Diogo & Tanaka, 2014)]; (ii) comparative anatomy including architecture, innervation, topology, and attachments; and (iii) distribution of muscles within the phylogeny of each group (see Diogo *et al.*, 2016, for detailed methods). Based on this evidence, the study concluded that the common ancestor of extant sarcopterygians probably had both superficial and deep dorsal and ventral muscle masses that extended from the girdles to the distal region of the fin, a series of even deeper dorsal and ventral muscles that spanned only a

few axial segments (similar to the pronators and supinators of *Latimeria*), and pre- and postaxial muscles that spanned more than one joint. The detailed one-to-one homologies Diogo *et al.* (2016) proposed between pectoral and pelvic appendicular muscles in the three taxa, including four muscles in the pectoral appendage of *Neoceratodus* and 19 muscles in the pectoral appendage of *Latimeria* (as compared to *Salamandra* or *Ambystoma*, Fig. 5; Table 2) allow us, for the first time, to use EPB to infer the presence of individual appendicular muscles in the pectoral appendage of extinct sarcopterygians, including early tetrapods.

### (1) Musculoskeletal anatomy of the pectoral fins of extant sarcopterygian fish

The musculoskeletal anatomy of the pectoral fins of extant sarcopterygian fish has previously been described in detail (e.g. Braus, 1900; Millot & Anthony, 1958; Diogo *et al.*, 2016; Miyake *et al.*, 2016), so here we will only summarize the



**Fig. 4.** Right pectoral girdles of the extant lobe-finned fish *Neoceratodus* (A, B), the extinct tetrapodomorph fish *Eusthenopteron* (C, D), and the extinct amniote *Archeria* (E, F) showing homologous regions between fish and tetrapods, according to Johanson *et al.* (2004) (in bold type). Lateral views on left, medial views on right.

relevant anatomy. In extant sarcopterygian fish, the pectoral skeleton consists of both endochondral (scapulocoracoid) and dermal (cleithrum, clavicle, anocleithrum) girdle elements, a series of axial elements ('mesomeres' *sensu* Ahlberg, 1989), preaxial and postaxial radials, and dermal fin rays (lepidotrichia or campotrichia) (Braus, 1900). The pectoral appendicular musculature consists of dorsal (adductor) and ventral (abductor) muscle masses (N.B., in extant lungfish and coelacanths the fin is rotated so that its dorsal surface lies against the body wall), subdivided into superficial and deep layers (Fig. 5A–D). The superficial layer originates on the girdle and inserts on the fin rays, and it is subdivided proximodistally by tendinous intersections that are attached to axial elements. The deep layer also originates on the girdle, but at least some portions insert more proximally on the fin.

#### (a) Extant coelacanths

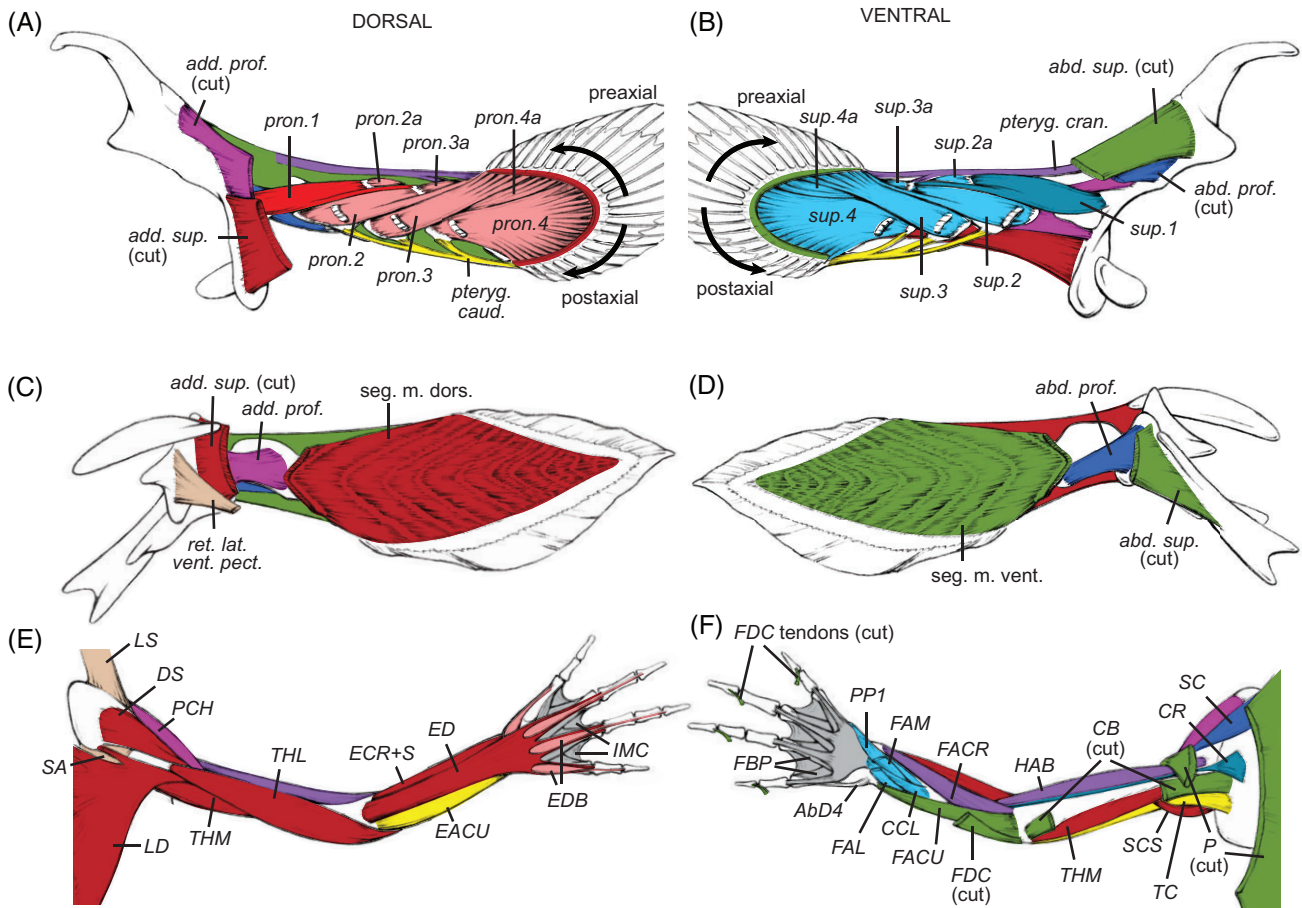
The pectoral appendicular muscle anatomy of extant coelacanths is more complex than that of lungfish (Fig. 5). The appendicular muscles in *Latimeria* originate entirely from the mesial aspect of the girdle (Millot & Anthony, 1958). In addition to superficial and deep adductors and abductors, thought to be homologous with similar muscles

in *Neoceratodus* (Fig. 5) (Diogo *et al.*, 2016), *Latimeria* has a preaxial muscle, a postaxial muscle, and a series of pronators and supinators (seven of each) that lie below the deep muscle layer and are oriented obliquely to the axis of the fin. The pronators and postaxial muscle are thought to be derived from the deep dorsal muscle mass, and the supinators and preaxial muscle from the deep ventral muscle mass; all were presumably secondarily lost during lungfish evolution along with the secondary reduction of the pectoral appendage of these fish (Diogo *et al.*, 2016). The evidence presented for secondary simplification (in the sense of having fewer individual muscles) of the pectoral fin in lungfish, including *Neoceratodus*, included: (i) similarities between the pelvic fin musculature of *Neoceratodus* and the musculature of both fins in *Latimeria* (Diogo *et al.*, 2016); (ii) similarities between the musculature of the pectoral fin in *Latimeria* and the pectoral limb in tetrapods (Diogo *et al.*, 2016); and (iii) the presence of a distinct radius and ulna in the pectoral fin of *Neoceratodus* at early developmental stages (Jude *et al.*, 2014), suggesting that the adult fin skeleton is secondarily simplified. The tendinous intersections that divide the superficial muscles attach to prominent ridges on the dorsal and ventral aspects of the axial elements, including the humerus and radius.

In *Latimeria*, the *adductor superficialis* originates from the posteromedial border of the cleithrum between the anocleithrum and scapulocoracoid (add. sup., Fig. 6G). Its counterpart on the ventral side, the *abductor superficialis*, originates from the medial face of cleithrum, extracleithrum and clavicle ventral to the glenoid (abd. sup., Fig. 6G). The *adductor* and *abductor profundus* originate from the medial face of the scapulocoracoid near the glenoid; the adductor – whose origin also includes part of the cleithrum – arises just dorsal to the glenoid, whereas the abductor arises just ventral to the glenoid (add. prof. and abd. prof., Fig. 6G). None of these four muscles leave osteological correlates on the girdle elements. Small ridges mark the dorsal and ventral borders of the glenoid, providing origins for *pronator 1* and *supinator 1*, respectively (pron. 1 and sup. 1, Fig. 6G) (see fig. 26 of Millot & Anthony, 1958).

The humerus of *Latimeria* is roughly cylindrical with a very prominent, blade-like ventral process and a smaller, rounded dorsal process (Fig. 6I, J). These processes provide attachments for the most proximal of the four tendinous intersections that divide the superficial adductor and abductors (Millot & Anthony, 1958; Miyake *et al.*, 2016). The pre- and postaxial borders of the humerus are marked by low ridges, and *pronator 2* and *supinator 2* originate from the dorsal and ventral aspects of the postaxial ridge, respectively (pron. 2 and sup. 2, Fig. 6I, J). No muscles attach to the preaxial ridge. *Supinator 1* and *pronator 1* insert partially on the distal, postaxial end of the humerus and partly on the joint capsule, radius, and ulna (sup. 1 and pron. 1, Fig. 6I, J).

The ulna in *Latimeria* is similar to the humerus in shape, although slightly smaller. Like the humerus, it has a very prominent ventral process and a smaller dorsal process which form attachments for the superficial adductor and abductor (add. sup. and abd. sup.; Fig. 6K, L). *Pronator 3* and



**Fig. 5.** Hypotheses of forelimb muscle homology from Diogo *et al.* (2016). (A, B) *Latimeria*, (C, D) *Neoceratodus*, and (E, F) *Ambystoma* in dorsal (A, C, E) and ventral (B, D, F) views. Colours indicate homologous muscles. Abbreviations: *abductor digiti minimi* (AbD4), *abductor profundus* (abd. prof.), *abductor superficialis* (abd. sup.), *adductor profundus* (add. prof.), *adductor superficialis* (add. sup.), *coracobrachialis* (CB), *contrahentium caput longum* (CCL), *coracoradialis* (CR), *deltoideus scapularis* (DS), *extensor antebrachii et carpi ulnaris* (EACU), *extensor carpi radialis + supinator* (ECR + S), *extensor digitorum* (ED), *extensores digitorum breves* (EDB), *flexor antebrachii et carpi radialis* (FACR), *flexor antebrachii et carpi ulnaris* (FACU), *flexor accessorius lateralis* (FAL), *flexor accessorius medialis* (FAM), *flexores breves profundi* (FBP), *flexor digitorum communis* (FDC), *humeroantebrachialis* (HAB), *intermetacarpales* (IMC), *latissimus dorsi* (LD), *levator scapulae* (LS), *palmaris profundus 1* (PP1), *pectoralis* (P), *procoracohumeralis* (PCH), *pronator 1, 2, 2a, 3, 3a, 4, 4a* (pron. 1–4a), *pterygialis caudalis* (pteryg. caud.), *pterygialis cranialis* (pteryg. cran.), *retractor lateralis ventralis pectoralis* (ret. lat. vent. pect.), *segmented muscle, dorsal* (seg. m. dors.), *segmented muscle, ventral* (seg. m. vent.), *serratus anterior* (SA), *subcoracoscapularis* (SCS), *supinator 1, 2, 2a, 3, 3a, 4, 4a* (sup. 1–4a), *supracoracoideus* (SC), *triceps coracoideus* (TC), *triceps humeralis lateralis* (THL), *triceps humeralis medialis* (THM), *triceps scapularis medialis* (TSM).

*supinator 3* originate from the dorsal and ventral aspects of the postaxial ridge, respectively. The radius is a small, oval element dorsal to the joint between the humerus and ulna. It does not articulate directly with any other bone, but it forms part of the insertions of *pronator 1* and *supinator 1* (pron. 1 and sup. 1, Fig. 6K, L).

#### (b) Extant lungfish

Like all extant lungfish, *Neoceratodus* has an entirely cartilaginous fin skeleton. It has only four pectoral appendicular muscles: a superficial adductor and superficial abductor that originate on the girdle and insert on the lepidotrichia, and a deep adductor and deep abductor that

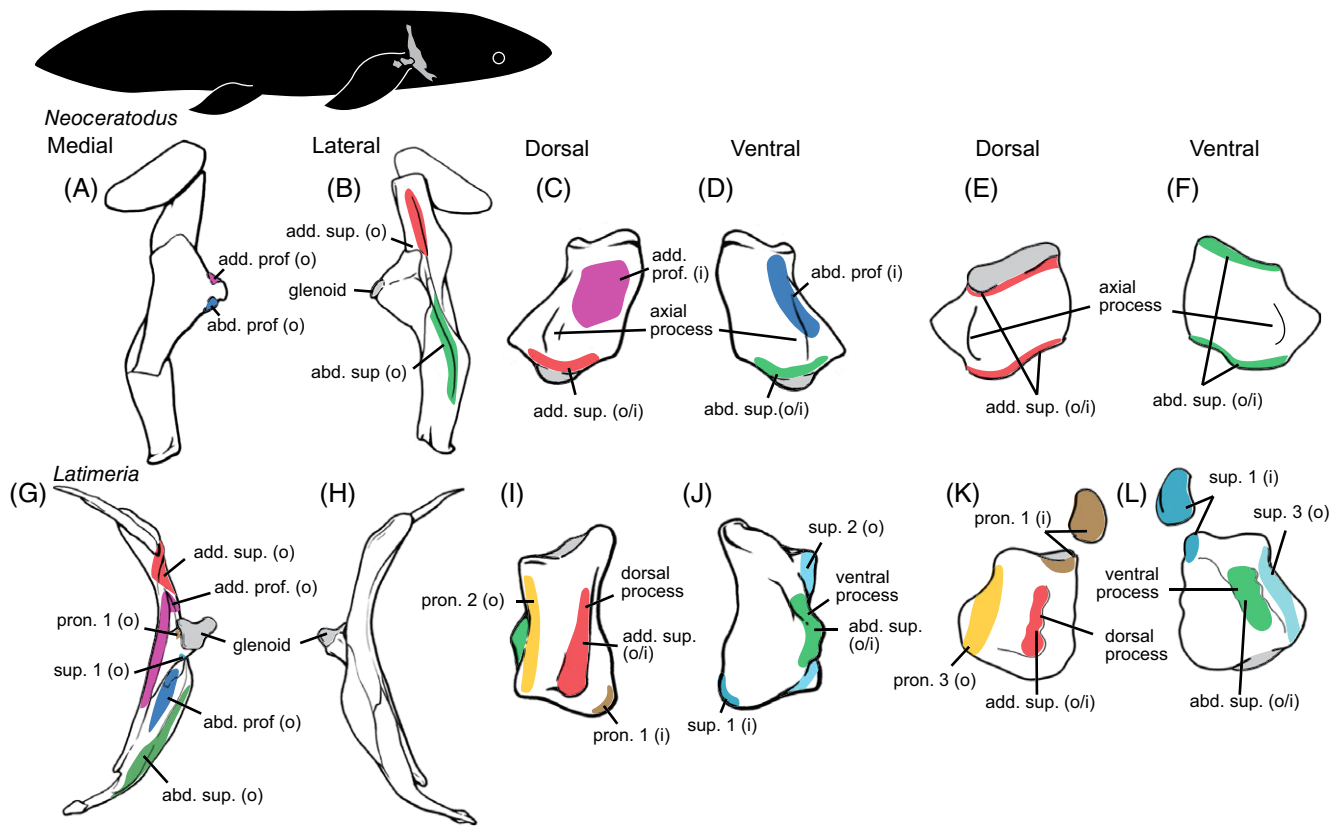
originate on the girdle and insert on the first axial element, homologous with the tetrapod humerus (add. prof. and abd. prof., Fig. 5C, D) (Braus, 1900; Diogo *et al.*, 2016). The tendinous intersections that divide the superficial muscle masses are attached to the joints between axial elements. Deep fibres of the superficial adductor and abductor fan out between the radials and insert on the lepidotrichia (add. sup. and abd. sup., Fig. 5C, D).

All four muscles that originate from the girdle in *Neoceratodus* leave osteological correlates (Fig. 6A, B). A longitudinal ridge on the external surface of the cleithrum and dorsal portion of the scapulocoracoid forms the origin of the *adductor superficialis*, and a similar ridge on the lateral aspect of the clavicle, cleithrum, and scapulocoracoid ventral to the

Table 2. Hypotheses of homology between pectoral appendicular muscles of *Latimeria*, *Neoceratodus*, *Salamandra*, and *Iguana* from Diogo, Ziermann, & Linde-Medina (2015); Diogo *et al.* (2016) and Diogo & Abdala (2010).

Muscle groups	<i>Latimeria</i>	<i>Neoceratodus</i>	<i>Salamandra</i>	<i>Iguana</i>
Superficial dorsomesial musculature	<i>Adductor superficialis</i> ('levator superficialis')	<i>Adductor superficialis</i> (including dorsal superficial segmented muscle layer)	<i>Deltoideus scapularis</i>	<i>Deltoideus scapularis</i>
			<i>Latissimus dorsi</i>	<i>Latissimus dorsi</i>
			<i>Extensor digitorum</i>	<i>Extensor digitorum</i>
			<i>Extensor antebrachii et carpi radialis</i>	<i>Extensor antebrachii et carpi radialis</i>
			<i>Triceps scapularis</i>	<i>Triceps scapularis</i>
			<i>Triceps humeralis lateralis</i>	<i>Triceps humeralis lateralis</i>
			<i>Triceps humeralis medialis</i>	<i>Triceps humeralis medialis</i>
			<i>Triceps coracoideus</i>	<i>Triceps coracoideus</i>
			<i>Extensor antebrachii et carpi ulnaris</i>	<i>Extensor antebrachii et carpi ulnaris</i>
			<i>Anconaeus</i>	
Deep dorsomesial musculature	<i>Adductor profundus</i> ('levator profundus')	<i>Adductor profundus</i>	<i>Procoracohumeralis</i>	<i>Deltoideus acromialis et clavicularis</i>
				<i>Scapulohumeralis anterior</i>
			<i>Subcorascapularis</i>	<i>Subscapularis</i>
				<i>Subcoracoideus</i>
			<i>Abductor et extensor digit 1</i>	<i>Abductor pollicis longus</i>
			<i>Extensores breves digitorum 2–4</i>	<i>Extensores breves digitorum 2–5</i>
Superficial ventrolateral musculature	<i>Abductor superficialis</i> ('abaisseur superficialis')	<i>Abductor superficialis</i> (including ventral superficial segmented muscle layer)	<i>Pectoralis</i>	<i>Pectoralis</i>
			<i>Flexor digitorum communis</i>	<i>Flexor digitorum longus</i> (superficial head)
			<i>Flexor antebrachii et carpi ulnaris</i>	<i>Flexor carpi ulnaris</i>
				<i>Epitrochleoanconeus</i>
			<i>Coracobrachialis</i>	<i>Coracobrachialis longus</i>
				<i>Coracobrachialis brevis</i>
			<i>Flexor antebrachii et carpi radialis</i>	<i>Flexor carpi radialis</i>
<i>Humeroantebrachialis</i>	<i>Brachialis</i>			
Deep ventrolateral musculature	<i>Abductor profundus</i> ('abaisseur profundus')	<i>Abductor profundus</i>	<i>Supracoracoideus</i>	<i>Supracoracoideus</i>
			<i>Coracoradialis</i>	<i>Biceps brachii</i>
			<i>Flexor accessorius medialis</i>	<i>Flexor digitorum longus</i> (deep head)
			<i>Palmaris profundus 1</i>	<i>Palmaris profundus 1</i>
			<i>Pronator quadratus</i>	<i>Pronator quadratus</i>
				<i>Pronator accessorius</i>
			<i>Supinator 1</i>	
			<i>Supinator 2</i>	
			<i>Supinator 2a</i>	–
			<i>Supinator 3</i>	<i>Flexor accessorius lateralis</i>
<i>Supinator 3a</i>	–			
<i>Supinator 4</i>	<i>Contraheantum caput longum</i>			
<i>Supinator 4a</i>	<i>Flexor digitorum longus</i> (deep head)			
	–			





**Fig. 6.** Muscle attachment areas on the right pectoral girdle (A, B, G, H), humerus (C, D, I, J), and radius/ulna (E, F, K, L) of *Neoceratodus* (top row) and *Latimeria* (bottom row) (modified from Millot & Anthony, 1958; Jude *et al.*, 2014; Miyake *et al.*, 2016). Origin (o) and insertion (i); colours and other abbreviations as in Fig. 5. Articular surfaces shaded in grey. Silhouette at top left shows configuration of pectoral girdle and proximal fin bones in *Neoceratodus*.

glenoid marks the origin of the *abductor superficialis* (add. sup. and abd. sup., Fig. 6B). Two facets on the scapulocoracoid mark the origins of the deeper muscles: one for the *adductor profundus* on the dorsal, scapular part just above the glenoid, and a second for the *abductor profundus* adjacent and ventral to the glenoid (add. prof. and abd. prof., Fig. 6A).

The humerus of *Neoceratodus* is a dorsoventrally flattened, L-shaped cartilage with small processes on its dorsal and ventral sides (axial process, Fig. 6C, D). The *adductor profundus* has a broad fleshy insertion on the dorsal surface of the humerus, proximal to the axial process, whereas the *abductor profundus* has a proximodistally long insertion on the postaxial half of the ventral surface (add. prof. and abd. prof., Fig. 6C, D) (Diogo *et al.*, 2016). Neither muscle leaves a skeletal correlate on the humerus. The dorsal and ventral processes probably provide attachments for the superficial adductor and abductor muscles (add. sup. and abd. sup., Fig. 6C, D), as in *Latimeria*, but we were unable to verify this.

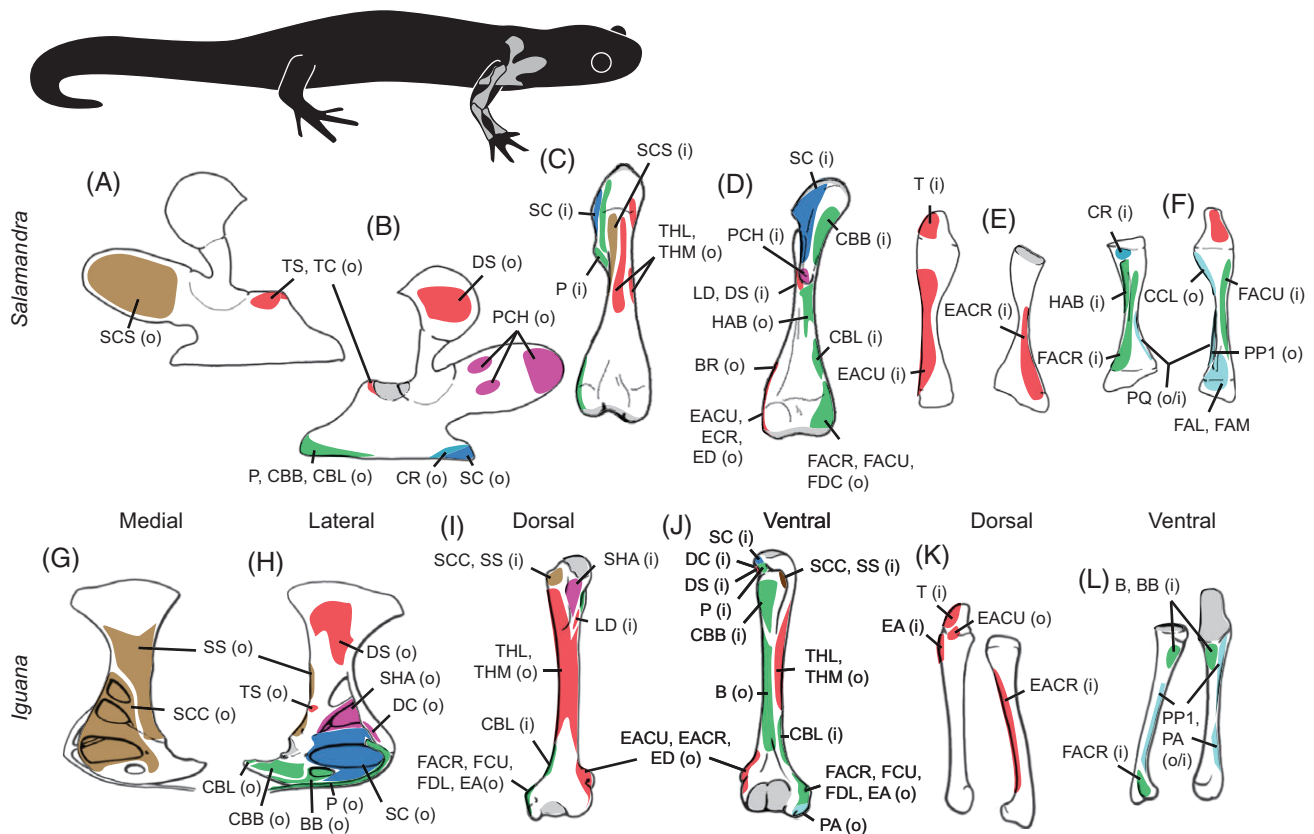
In *Neoceratodus* the radius merges with the ulna during embryonic development to form a broad, dorsoventrally flattened cartilage (Fig. 6E, F). It has axial processes similar to those on the humerus, but again we could not confirm that the tendinous intersections of the superficial adductor and abductor attach to these processes. The segmented portions

of the superficial muscles do attach to the joint capsules between the humerus and the radius/ulna and the joint between the radius/ulna and the subsequent axial element (add. sup. and abd. sup., Fig. 6E, F) (Braus, 1900).

## (2) Musculoskeletal anatomy of the pectoral limbs of extant tetrapods

The two extant clades of tetrapods, Lissamphibia and Amniota, diverged during the Carboniferous period, perhaps only a few million years after the end of the Devonian, around 355 MYA (Clack *et al.*, 2016). Other analyses have placed the amphibian–amniote divergence slightly earlier (360–355 MYA; Ruta & Coates, 2007) or later (340–342 MYA; Carroll, 2012). The limbs of generalized lizards and salamanders such as those we considered here share many of the same muscles. Diogo & Abdala (2010) reviewed the myology of key tetrapod taxa and provided an updated list of homology hypotheses, based on comparative anatomy and developmental data, between the pectoral appendicular muscles of vertebrates, including *Salamandra* and *Iguana* (Table 2).

Most lizard and salamander species share a suite of forelimb skeletal elements including the scapula, coracoid,



**Fig. 7.** Muscle attachment areas on the right pectoral girdle (A, B, G, H), humerus (C, D, I, J), and radius/ulna (E, F, K, L) of *Salamandra* and *Iguana* (modified from Miner, 1925; Francis, 1934; Dilkes, 1999). Colours as in Fig. 5. Abbreviations: *biceps brachii* (BB), *brachialis* (B), *brachioradialis* (BR), *contrahentium caput longum* (CCL), *coracobrachialis brevis* (CBB), *coracobrachialis longus* (CBL), *coracoradialis* (CR), *deltoideus clavicularis* (DC), *deltoideus scapularis* (DS), *epitrochleoanconeus* (EA), *extensor carpi radialis* (ECR), *extensor antebrachii et carpi radialis* (EACR), *extensor antebrachii et carpi ulnaris* (EACU), *extensor digitorum* (ED), *flexor antebrachii et carpi radialis* (FACR), *flexor antebrachii et carpi ulnaris* (FACU), *flexor carpi ulnaris* (FCU), *flexor accessorius lateralis* (FAL), *flexor accessorius medialis* (FAM), *flexor digitorum communis* (FDC), *flexor digitorum longus* (FDL), *humeroantebrachialis* (HAB), insertion (i), *latissimus dorsi* (LD), origin (o), *palmaris profundus I* (PP1), *pectoralis* (P), *procoracohumeralis* (PCH), *pronator accessorius* (PA), *pronator quadratus* (PQ), *scapulohumeralis anterior* (SHA), *subcoracoideus* (SCC), *subcoracoscapularis* (SCS), *subscapularis* (SS), *supracoracoideus* (SC), *triceps* (T) [*coracoideus* (-C), *humeralis lateralis* (-HL), *humeralis medialis* (-HM) and *scapularis* (-S)]. Articular surfaces shaded in grey. Silhouette at top left shows configuration of pectoral girdle and limb bones in *Salamandra*.

clavicle, humerus, radius, ulna, carpals, metatarsals, and phalanges. Additional girdle elements are present in some taxa (cartilaginous procoracoid in salamanders including *Salamandra*, bony interclavicle and epicoracoid in lizards including *Iguana*), and the two clades are characterized by different numbers of carpals and digits (Francis, 1934; Russell & Bauer, 2008). Although the girdle in *Iguana* is ossified except for the suprascapula and part of the procoracoid, the girdle in *Salamandra* is entirely cartilaginous except for the scapula. However, there is no reason to expect that this difference affects the attachments of muscles.

#### (a) Salamanders (Urodela)

The anatomy of *Salamandra salamandra* will be described as a representative of salamanders (which in turn represent Lissamphibia), and differences from *Ambystoma mexicanum* and other salamanders will be noted. The dorsal shoulder muscles

in *Salamandra* originate from the scapula, suprascapula, and part of the internal coracoid and procoracoid (Fig. 7A, B) (Francis, 1934). The *deltoideus* originates from the dorsolateral surface of the cartilaginous suprascapula (DS, Fig. 7B). The *triceps* originates from the scapula at the posterior margin of the glenoid (scapular head) and the posterior extreme of the coracoid (coracoid head) (TS and TC, Fig. 7B). In the aquatic salamander *Necturus maculosus*, the origin of the coracoid head of the *triceps* is marked by a tuberosity (Chen, 1935). The *subcoracoscapularis* and *procoracohumeralis* originate from the internal surface of the procoracoid cartilage (SCS and PCH, Fig. 7A, B). The ventral shoulder muscles originate from the external coracoid (*supracoracoideus* and *coracoradialis* from the anterior portion and *coracobrachialis brevis* from the posterior portion) and sternum (*pectoralis*) (SC, CR, CB, and P, Fig. 7B). The *coracobrachialis longus* shares an origin with the coracoid head of the dorsal *triceps* muscle (CBL, Fig. 7B).

The humerus in *Salamandra* is characterized by four main osteological correlates: on the proximal portion of the bone are the deltopectoral crest (also known as crista ventralis or processus lateralis humeri), which forms the insertion for the *deltoideus*, *pectoralis*, *procoracohumeralis*, and *supracoracoideus*, and the crista dorsalis (processus medialis humeri), which forms the insertion of the *subcoracoscapularis* (DS, P, PCH, SC, and SCS, Fig. 7C, D). On the distal end of the bone are the entepicondyle (medial epicondyle), which forms the origin of the forearm flexors; and the ectepicondyle (lateral epicondyle), which forms the origin of the forearm extensors. In addition, *Salamandra* has five muscles that attach to the humerus without leaving individual correlates. The dorsal shoulder muscle *latissimus dorsi* inserts on the anterolateral border of the humerus in *Salamandra* (LD, Fig. 7D) (Francis, 1934) and on the deltopectoral crest in *Ambystoma* (Diogo & Tanaka, 2012). The ventral shoulder muscles *coracobrachialis longus* and *brevis* insert on the posterior face of the humerus (CBL and CBB, Fig. 7D). The dorsal arm muscle *humeroantebrachialis* originates from the ventral aspect of the humerus just distal to the deltopectoral crest in *Salamandra* (HAB, Fig. 7D) (Francis, 1934) and from the deltopectoral crest in *Necturus* (Chen, 1935). Finally, the medial and lateral heads of the dorsal arm muscle *triceps humeralis* originates from most of the dorsal (extensor) surface and part of the anterolateral surface of the humerus (THM and THL, Fig. 7C) (Francis, 1934).

Compared with the humerus, very few osteological correlates are present on the radius and ulna in *Salamandra*. The most obvious is the olecranon process of the ulna, which forms the insertion of the *triceps* complex (T, Fig. 7E). In addition to the olecranon process, the ulna in *Salamandra* has a ventral ridge near its distal end (Francis, 1934), located in the same region as the origins of the *pronator quadratus*, *flexor accessorius lateralis*, and *flexor accessorius medialis* (PQ, FAL and FAM, Fig. 7F). Likewise, the radius bears a ventral process on the proximal end of the ventral (flexor) side (Francis, 1934), in the same region as the insertion of the *humeroantebrachialis* (HAB, Fig. 7F). The remaining muscles do not leave osteological correlates. The radius provides insertions for the *extensor antebrachii et carpi radialis* on the dorsal radial aspect, *flexor antebrachii et carpi radialis* on the ventral radial aspect, and *pronator quadratus* ('interossei antebrachii') on the ulnar aspect (EACR, FACR, and PQ, Fig. 7E, F) (Francis, 1934). Similarly, the ulna provides insertions for the *extensor antebrachii et carpi ulnaris* on the dorsal ulnar aspect, *flexor antebrachii et carpi ulnaris* on the ventral ulnar aspect, and the origins of the *pronator quadratus* and *palmaris profundus I* ('pronator profundus') on the radial aspect (FACU, PQ, and PPI, Fig. 7E, F). The proximal ventral radius provides the insertion for the *coracoradialis* (CR, Fig. 7F). The proximal radial, distal ventral, and distal radial surfaces of the ulna provide origins for the deep digital flexors *contrahentium caput longum*, *flexor accessorius lateralis*, and *flexor accessorius medialis*, respectively (CCL, FAL, and FAM, Fig. 7F) (Francis, 1934). In the giant salamander *Andrias japonicus* (*Megalobatrachus maximus*), the distal ulna gives origin to the *abductor et extensor*

*D1* (Miner, 1925), but this muscle originates from the carpals in *Salamandra* (Francis, 1934). It is conceivable that these differences are due to subjective interpretations; a careful synthesis of appendicular myology across Urodela/Caudata is needed.

#### (b) Lizards (Squamata)

In this section, the muscle anatomy of *Iguana iguana* is described as a representative of plesiomorphic extant amniotes, with differences from the lepidosaur *Sphenodon punctatus* and other squamates noted. Compared with *Salamandra*, *Iguana* has six additional pectoral appendicular muscles: (i) *scapulohumeralis anterior* and *deltoideus clavicularis* rather than *procoracohumeralis*; (ii) *subcoracoideus* and *subscapularis* rather than *subcoracoscapularis*; (iii) *coracobrachialis longus* and *brevis* rather than *coracobrachialis*; (iv) *abductor pollicis longus* and *extensor brevis pollicis* rather than *abductor et extensor pollicis*; (v) *flexor carpi ulnaris* and *epitrochleoanconeus* rather than *flexor antebrachii et carpi ulnaris*; and (vi) *pronator accessorius* in addition to *pronator quadratus* (Fig. 7G–L; Table 2). Also, the four muscles *flexor digitorum communis*, *contrahentium caput longum*, *flexor accessorius lateralis*, and *flexor accessorius medialis* are fused to form the *flexor digitorum longus* (FDL, Fig. 7I, J). The *extensor antebrachii ulnaris* and *extensor carpi ulnaris* are fused to form the *extensor antebrachii et carpi ulnaris* (EACU, Fig. 7I, J); these two muscles are separate in *Sphenodon*. *Iguana* does not have a separate *anconeus*, but this muscle is present in some other lepidosaurs, including *Sphenodon* (Diogo *et al.*, 2009).

The dorsal shoulder muscles in *Iguana* originate not only from the scapula, suprascapula, and internal coracoid, as they do in *Salamandra*, but also from the epicoracoid and clavicle (Russell & Bauer, 2008) (Fig. 7G, H). The *deltoideus scapularis* originates more ventrally from the external surface of the ossified part of the scapula (DS, Fig. 7H). The *triceps* originates from the scapula just above the glenoid (scapular head; TS, Fig. 7H) and the sternoscapular ligament (coracoid head); the *triceps* does not leave an osteological correlate on the pectoral girdle in *Iguana*. The two homologues of the *subcoracoscapularis* originate from the epicoracoid, coracoid, and part of the scapula (*subcoracoideus*) and the medial aspect of the scapula and suprascapular cartilage (*subscapularis*) (SCC and SS, Fig. 7G). The two homologues of the *procoracohumeralis* originate from the lateral aspect of the scapula (*scapulohumeralis anterior*) and the medial portion of the clavicle (*deltoideus clavicularis*) (SHA and DC, Fig. 7H). The ventral shoulder muscles originate from the external aspect of the coracoid and sternum, as in *Salamandra*, as well as the interclavicle and epicoracoid. The *pectoralis* originates from the sternum, costal ribs, and posterior and lateral processes of the interclavicle, leaving two of the three identifiable osteological correlates on the pectoral girdle of *Iguana* (P, Fig. 7H). The *biceps brachii*, the homologue of the *coracoradialis* in *Salamandra* (Diogo & Abdala, 2010), likewise originates from the external aspect of the coracoid (BB, Fig. 7H). The *supracoracoideus* originates from the external aspect of the coracoid and epicoracoid (SC, Fig. 7H). The *coracobrachialis longus* originates from the posterior coracoid process and the



*coracobrachialis brevis* originates from the external aspect of the coracoid (CBL and CBB, Fig. 7H).

The humeral muscle attachments and osteological correlates in *Iguana* are similar to those in *Salamandra*, with a few slight differences. In *Iguana*, a distinct tuberosity on the deltopectoral crest marks the insertion of the *supracoracoideus*, and a slight prominence marks the insertion of the *latissimus dorsi* (SC and LD, Fig. 7I, J). Two concavities on the dorsal aspect of the humerus mark the origins of the *triceps humeralis lateralis* and *medialis* (Russell & Bauer, 2008) (THL and THM, Fig. 7I, J). Three other small differences also exist: as in *Necturus*, the origin of the *humeroantibrachialis* (brachialis) includes part of the deltopectoral crest in *Iguana* (B, Fig. 7J), and the *scapulohumeralis anterior*, one of the two homologues of the *procoracohumeralis*, inserts separately just proximal to the *latissimus dorsi* (Russell & Bauer, 2008) (SHA, Fig. 7I). One head of the *pronator accessorius*, a derivative of the ancestral *pronator quadratus*, originates from the ectepicondyle.

The only potential osteological correlates identified by Russell & Bauer (2008) on the radius and ulna in *Iguana* are the olecranon process, which provides the insertion of the *triceps*, and the posterior fossa of the ulna, which provides the bony origin of the *pronator accessorius* and *palmaris profundus I* ('pronator profundus') (T, PA, and PP1, Fig. 7K, L). In our dissections of *Sphenodon*, we observed proximal ventral processes on the radius and ulna associated with the insertions of the *brachialis* and *biceps brachii* (B and BB, Fig. 7L). Similar correlates in stem reptiles have also been interpreted in this way (e.g. captorhinids; Holmes, 1977).

### III. REVIEW OF OSTEOLOGICAL CORRELATES IN FOSSIL SARCOPTERYGIANS

We identified fossil taxa to include in our analysis based on phylogenetic position and the availability of detailed descriptions, illustrations, photographs, and/or specimens or casts for direct observation (Table 3). We included a representative selection of tetrapodomorph fish and stem tetrapods for which sufficient appendage information was available because these groups are closest to the fins-to-limbs (and water–land) transition. We also included several non-tetrapodomorph sarcopterygians from the lineages leading to lungfish and coelacanths to help distinguish which characteristics of extant lobe-finned fishes are common to all sarcopterygians, as well as several stem amphibians and reptiles.

#### (1) Pectoral girdle

##### (a) *Onychodontids and dipnomorphs*

The pectoral girdle in onychodontids and dipnomorphs has some osteological correlates suggestive of similar musculature to that of coelacanths and extant lungfish, including scars or facets adjacent to the glenoid and longitudinal ridges or thickenings on the dermal girdle (Fig. 8A). On the

scapulocoracoid of *Onychodus* is a medially facing facet that may have been an area for muscle attachment (mf, Fig. 8A), and there is a thickening on the medial side of the girdle running anteroventrally from the scapulocoracoid towards the anterior ventral tip of the cleithrum (Andrews *et al.*, 2005). Muscle scars are present adjacent to the glenoid both dorsally and ventrally in the fossil lungfish *Chirodipterus* (fig. 3B of Johanson *et al.*, 2004), similar to the areas of origin of the *adductor* and *abductor superficialis* in *Neoceratodus*. No osteological correlates were described on the pectoral girdle of *Pentlandia* or *Glyptolepis* (Ahlberg, 1989; Jude *et al.*, 2014).

##### (b) *Tetrapodomorph fish*

Rhizodontids are the earliest-diverging tetrapodomorphs (i.e. taxa more closely related to crown tetrapods than to extant lungfish) in our analysis. Their pectoral girdle is similar to that of the non-tetrapodomorph sarcopterygians, both extant and extinct, and similar osteological correlates are present. As in *Chirodipterus* and *Neoceratodus*, muscle scars are present on the scapulocoracoid adjacent to the glenoid, located dorsally in *Strepsodus* (cr, Fig. 8C) (Parker *et al.*, 2005) and ventromesially in *Barameda* (fig. 5 of Holland, 2013). The scapulocoracoid has a dorsal process in *Strepsodus* (dp, Fig. 8C) (Parker *et al.*, 2005) and *Sauripterus* (Davis *et al.*, 2004). The cleithrum of *Sauripterus* exhibits an anteroposteriorly oriented ridge ('ventral cleithral ridge'), interpreted as a possible origin for the pectoralis musculature (Davis *et al.*, 2004). A flange on the posterior edge of the cleithrum in *Strepsodus* (pf, Fig. 8B) and *Megalichthys* was suggested to be the origin of the *latissimus dorsi* (Andrews & Westoll, 1970a,b), but it might just as easily form the origin of an undifferentiated superficial adductor like that of extant lobe-finned fish.

In the more-crownward tetrapodomorphs *Gogonasmus* and *Eusthenopteron*, additional scars on the scapulocoracoid may reflect the beginning of shoulder muscle differentiation. In *Gogonasmus*, the dorsal process of the scapula bears faint grooves, possibly for muscle attachment (Holland, 2013). The scapulocoracoid of *Gogonasmus* has a crest on the ventromedial aspect of the anterior buttress (corresponding to the coracoid crest in rhizodontids) with a probable muscle attachment scar and a knob-like process on the ventral side between the anterior and posterior buttresses (Holland, 2013). In *Eusthenopteron*, two small pits located on a similar part of the scapulocoracoid were interpreted as the origin of the *coracobrachialis* (cb?, Fig. 8E), and a hollow just dorsal to the glenoid as the origin of the *procoracohumeralis* (sh, Fig. 8E) ('scapulohumeralis', Andrews & Westoll, 1970a). Like *Sauripterus*, *Gogonasmus* has a 'ventral cleithral ridge', and *Eusthenopteron* has a similar ridge (vcr, Fig. 8E) (Holland, 2013) which was interpreted as the anterior extent of the pectoralis origin in the latter taxon (Andrews & Westoll, 1970a). The cleithrum in *Eusthenopteron* also has a thickened posterior margin just above the glenoid (del?, Fig. 8E) which was interpreted as the origin of the *deltoideus* and part of the *latissimus dorsi* (Andrews & Westoll, 1970a).

The most-crownward tetrapodomorphs we reviewed, *Panderichthys* and *Tiktaalik*, reveal few clues about the



Table 3. Fossil taxa and specimens included in this study. Institutional abbreviations: Academy of Natural Sciences of Philadelphia (ANSP), Geological Museum of the University of Copenhagen (MGUH), Museum of Comparative Zoology, Harvard (MCZ), Natural History Museum, London (BMNH), University of Glasgow Hunterian Museum (GLAHM).

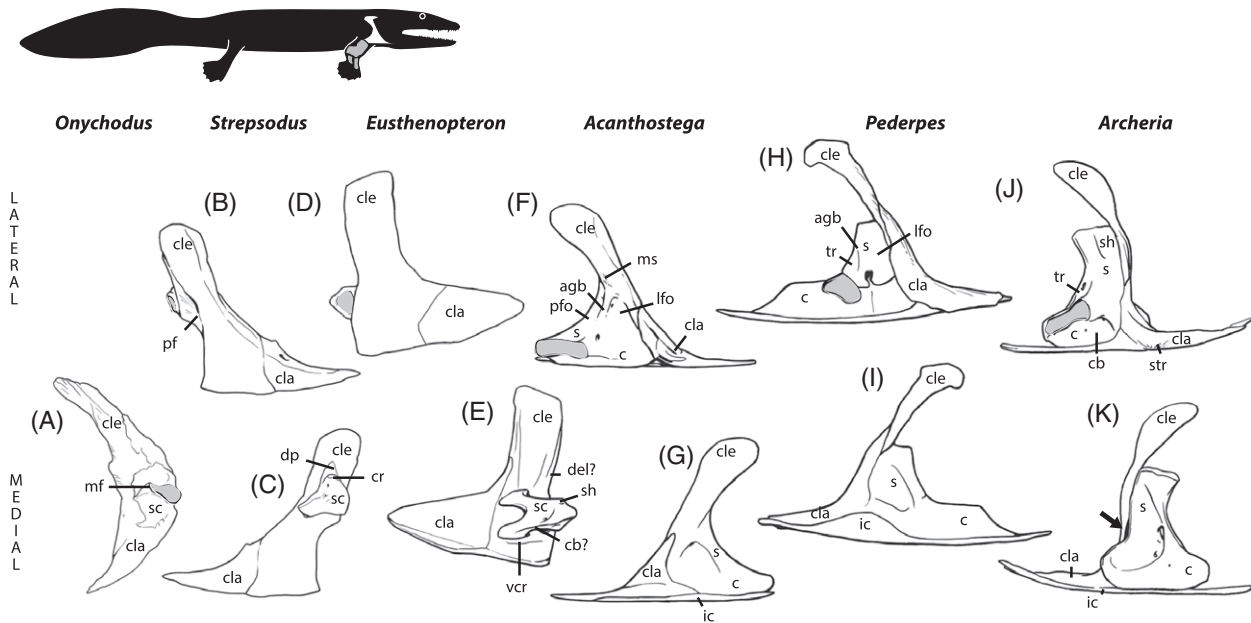
Species	Clade	Specimen(s) examined	References
<b>Non-tetrapodomorph sarcopterygians</b>			
<i>Onychodus jandemarra</i>	Onychodontidae		Andrews <i>et al.</i> (2005)
<i>Chirodipterus australis</i>	Dipnomorpha		Johanson <i>et al.</i> (2004)
<i>Pentlandia macroptera</i>	Dipnomorpha		Jude <i>et al.</i> (2014)
<i>Glyptolepis</i> sp.	Dipnomorpha		Ahlberg (1989)
<b>Tetrapodomorph fish</b>			
<i>Strepsodus</i> (multiple species)	Rhizodontida		Jeffery (2001) and Parker, Warren & Johanson (2005)
<i>Barameda decipiens</i>	Rhizodontida		Long (1989), Garvey, Johanson & Warren (2005) and Holland (2013)
<i>Rhizodus hibberti</i>	Rhizodontida		Jeffery (2001)
<i>Sauripterus taylori</i>	Rhizodontida		Davis, Shubin & Daeschler (2004)
<i>Aztecia mahalae</i> (' <i>Notorhizodon</i> ')	Rhizodontida		Young, Long & Ritchie (1992) and Johanson & Ahlberg (2001)
<i>Rhizodopsis sauroides</i>	Osteolepidida		Andrews & Westoll (1970b)
<i>Sterropterygion brandei</i>	Osteolepidida		Thompson (1972) and Rackoff (1980)
<i>Gogonasmus andrewsae</i>	Osteolepidida		Boisvert (2009) and Holland (2013)
<i>Eusthenopteron foordi</i>	Osteolepidida	NHMUK P 6794, P 6806, P 60391a, P 6797	Andrews & Westoll (1970a) and Boisvert (2009)
<i>Panderichthys rhombolepis</i>	Elpistostegalia		Shubin <i>et al.</i> (2006), Boisvert (2009) and Ahlberg (2011)
<i>Tiktaalik roseae</i>	Elpistostegalia	MCZ casts of NUFV 109 and NUFV 112	Shubin <i>et al.</i> (2006), Boisvert (2009) and Ahlberg (2011)
<b>Stem tetrapods</b>			
'Catskill humerus' (ANSP 21350)	Stegocephalia	MCZ cast of ANSP 21350	Shubin <i>et al.</i> (2004) and Ahlberg (2011)
<i>Acanthostega gunnari</i>	Stegocephalia	MGUH 1227, fn260, T1291, fn272, 1258, 1300	Coates (1996) and Ahlberg (2011)
<i>Ichthyostega</i> (multiple species)	Stegocephalia		Panchen (1985), Jarvik (1996), Callier <i>et al.</i> (2009) and Ahlberg (2011)
<i>Hynerpeton bassetti</i>	Stegocephalia	MCZ cast of ANSP 20901	Daeschler <i>et al.</i> (1994)
<i>Tulerpeton curtum</i>	Stegocephalia		Lebedev & Coates (1995)
<i>Crassigyrinus scoticus</i>	Stegocephalia		Panchen (1985)
<i>Ossinodus pueri</i>	Whatcheeriidae		Bishop (2014)
<i>Pederpes finneyae</i>	Whatcheeriidae	GLAHM 100815	Clack & Finney (2005)
<i>Whatcheeria deltae</i>	Whatcheeriidae		Lombard & Bolt (1995)
<i>Greerepeton burkemorani</i>	Colosteus	MCZ 9006	Godfrey (1989)
<i>Baphetes</i> (multiple species)	Baphetidae		Milner & Lindsay (1998)
<b>Extinct tetrapods within the crown group</b>			
<i>Archeria</i> (multiple species)	Embolomeri	MCZ 2047, 2045, 2049	Romer (1957)
<i>Eoherpeton watsoni</i>	Embolomeri		Smithson (1985)
<i>Eryops</i> (multiple species)	Eryopoidea	MCZ 7784, 2615, 2583, 7778, 1421, 1744, KU 33R, 1228, 2685, 7783, 2565	Miner (1925) and Pawley & Warren (2006)
Captorhinids (multiple taxa)	Eureptilia		Holmes (1977)

evolution of tetrapod shoulder musculature. In *Tiktaalik*, paired sulci on the internal and external margins of the coracoid foramen are interpreted as correlates of a musculotendinous bundle passing from the dorsomedial portion of the coracoid to the ventral humerus (Shubin *et al.*, 2006). We examined the cast and observed faint rugosities above the glenoid and a hollow above the coracoid foramen (Table 3, NUFV 112; see online Supporting Information, Fig. S1C) that would have been well placed for the origins of deep dorsal musculature. No features commonly associated with muscle attachment, such as ridges

or rugosities, were described on the pectoral girdle of *Panderichthys* (Vorobyeva, 1995). However, the fossil shows a ventral and posterior expansion of the coracoid plate, lacking in other tetrapodomorph fish such as *Eusthenopteron* (Vorobyeva, 1995), which may have served as the origin of muscles that adduct the fin at the shoulder.

#### (c) *Stem tetrapods*

The scapulocoracoid in stem tetrapods often exhibits posterior and lateral concavities, sometimes with muscle attachment scars, separated by the ridge known as the



**Fig. 8.** Right pectoral girdles of the onychodontid *Onychodus* (A), the tetrapodomorph fishes *Strepsodus* (B, C) and *Eusthenopteron* (D, E) the stem tetrapods *Acanthostega* (F, G) and *Pederpes* (H, I), and the embolomere *Archeria* (J, K) (modified from Andrews *et al.*, 2005; Parker *et al.*, 2005; Andrews & Westoll, 1970a; Coates, 1996; Clack & Finney, 2005; Romer, 1957). Abbreviations: anterior glenoid buttress (agb), clavicle (cla), cleithrum (cle), coracobrachialis origin (cb), coracoid portion of scapulocoracoid (c), crest (cr), deltoideus origin (del), dorsal process (dp), interclavicle (ic), lateral fossa (lfo), medially facing facet (mf), muscle scar on cleithrum (ms), posterior flange (pf), posterior fossa (pfo), scapular portion of scapulocoracoid (s), scapulocoracoid (sc), scapulohumeralis depression (sh), striations (str), triangular region (tr), ventral cleithral ridge (vcr). Black arrow in K indicates gap between coracoid plate and clavicle that may have housed the *supracoracoideus*. Glenoid shaded in grey. Silhouette at top left shows configuration of pectoral girdle and limb bones (girdle in white) in *Acanthostega gunnari*.

anterior glenoid buttress (agb, Fig. 8F, H). These correlates suggest two separate deep dorsal muscles, probably the *subcoracoscapularis* and *procoracohumeralis*, with different lines of action. Scars on the posterior or lateral edge of the cleithrum and/or clavicle probably represent the origins of superficial dorsal muscles such as the *deltoideus* and/or *latissimus dorsi*. Few stem-tetrapod fossils preserve the ventral edge of the coracoid plate, so the origins of ventral musculature could not be definitively traced; however, we tentatively accept that scars on the ventral surface of the interclavicle, distinct from the dermal ornament, may mark part of the origin of superficial ventral muscles such as the *pectoralis*.

We reviewed four tetrapods from the Devonian with well-preserved pectoral girdle elements: *Acanthostega gunnari*, *Ichthyostega* spp., *Tulerpeton curtum*, and *Hynierpeton bassetti*. In the former two taxa, the glenoid is directed posterolaterally and the scapula extends only slightly dorsal to the glenoid (Fig. 8F) (Coates, 1996; Jarvik, 1996). Similarly, the scapula extends only slightly dorsal to the glenoid in *Hynierpeton* (see fig. 1 of Daeschler *et al.*, 1994). No potential muscle attachments are described on the scapulocoracoid in either *Ichthyostega* or *Acanthostega*, but a distinct depression just ventral to the anteroventral process at the junction of the cleithrum and scapulocoracoid is described in *Ichthyostega* (Jarvik, 1996). In *Acanthostega* we observed posterior and lateral fossae on the scapulocoracoid dorsal to the glenoid (pfo and lfo, Fig. 8F; MGUH 1258, 1300, Fig. S1B) similar to the areas described

as muscle origins in more crownward taxa. On the cleithrum of *Acanthostega*, a muscle scar is present on the lateral surface just dorsal to the anteroventral process which forms part of the articulation with the clavicle (Coates, 1996) (ms, Fig. 8F). In *Tulerpeton*, a rugose area above the glenoid was suggested as the origin of the *subcoracoscapularis*, and tubercles were noted on the posterior edge of the clavicle (Lebedev & Coates, 1995). In *Hynierpeton*, rugose ridges thought to be muscle scars were described on the dorsal border of the subscapular fossa (Daeschler *et al.*, 1994). Also in *Hynierpeton*, a broad, shallow fossa, bounded anteriorly by a rugose ridge, is interpreted as the origin for limb elevators and protractors (Daeschler *et al.*, 1994). These two features are not found in other Devonian tetrapods, suggesting that they reflect an unusual functional specialization or early development of powerful forelimb muscles with support and/or locomotor capabilities (Daeschler *et al.*, 1994).

The remaining stem tetrapods with well-preserved pectoral girdle elements date from the Carboniferous: the colosteid *Greererpeton burkemorani*, the whatcheeriids *Pederpes finneyae* and *Ossinodus pueri*, and *Crassigyrinus scoticus*. In *Ossinodus*, Bishop (2014) documented and described the extraordinary preservation of attachment scars of what may be individual muscle fascicles, which appear as fine, elongated pits and/or anastomosing ridges. These scars cover distinct areas of the bones and were interpreted as attachments of individual muscles based on comparative literature on

tetrapod myology, particularly the studies of Miner (1925) and Romer (1922). An area of scarring covering the entire posterior face of the scapulocoracoid above the glenoid and much of its internal aspect was interpreted as the origin of the *subcoracoscapularis* ('subscapularis'; Bishop, 2014). In *Ossinodus*, an area of scarring that covers a large, shallow concavity on the lateral face of the scapulocoracoid was interpreted as the origin of the *procoracohumeralis* ('scapulohumeralis'; Bishop, 2014). Longitudinally oriented, anastomosing ridges and grooves along the posterior margins of the cleithrum and clavicle, including the ascending process of the clavicle, were interpreted as the origin of the *deltoideus* (Bishop, 2014). In *Crassigyrinus*, the inner surface and ascending process of the clavicle also show striations and longitudinal grooves (Panchen, 1985). Finally, a rugose, slightly recessed region on the posterior lateral wings of the interclavicle was interpreted as part of the origin of the *pectoralis* (Bishop, 2014). In *Pederpes*, the coracoid is not preserved, and no muscle scars are described on the scapula, clavicle, or cleithrum (Clack & Finney, 2005). However, on the scapula we observed a lateral fossa and a posterior triangular region (lfo and tr, Fig. 8H; Fig. S1A) that were similar to the correlates interpreted as origins of the *procoracohumeralis* and *subscapularis*, respectively, in *Ossinodus* by Bishop (2014). A complete pectoral girdle of *Greererpeton* was reconstructed based on multiple specimens by Godfrey (1989). A ridge on the scapula bounding an excavated posterior region and a thickened posterior margin were described, as well as conspicuous striations on the tip of the ascending process of the clavicle. Striations were also noted on the external margin of the interclavicle, distinct from the dermal ornamentation (Godfrey, 1989).

#### (d) Crown tetrapods

The fossil crown tetrapod genera we surveyed were: *Eryops*, *Eoherpeton*, *Archeria*, and *Captorhinus*. Although the skeleton of the Permian temnospondyl *Eryops* is extremely well ossified compared with that of modern lissamphibians, its pectoral girdle exhibits few obvious osteological correlates of muscle attachment. However, a concave region above the glenoid ('supraglenoid fossa'; Pawley & Warren, 2006), similar to the lateral fossa in stem tetrapods, was interpreted as the origin of the *subcoracoscapularis* (Miner, 1925), and we observed ridges and rugosities in this region (MCZ 2615, 2565, 2583, Fig. S1E).

Many more individual osteological correlates have been described on the pectoral girdle in stem amniotes than in the extant amniotes we studied (likely because this evidence is of great importance for palaeontologists, and also because extinct tetrapods encompass greater morphological diversity), including those associated with the *subcoracoscapularis*, *procoracohumeralis*, and *deltoideus* in stem tetrapods, as well as a convincing origin for the *coracobrachialis longus* and, possibly, *triceps*, as described below. Unlike in *Iguana* and other lizards, the scapula and coracoid in the fossil stem and crown amniotes we surveyed are not separately ossified (although sutures are visible in immature captorhinids; Holmes, 1977). On the scapulocoracoid of

*Eoherpeton*, *Archeria*, and captorhinids, a triangular area above the glenoid was interpreted as the origin of the *subcoracoscapularis* (tr, Fig. 8J) (Romer, 1957; Holmes, 1977; Smithson, 1985). A tubercle in this area was interpreted by Smithson (1985) as a primary attachment for this muscle in *Eoherpeton*, but Bishop (2014) suggested that it instead marks the scapular origin of the *triceps*. We used the second interpretation in our analysis because it seems unlikely that a muscle like the *subcoracoscapularis* that has such an extensive area of origin in both *Salamandra* and *Iguana* (SCS, Fig. 7A; SS plus SC, Fig. 7G) would leave such a small correlate in *Eoherpeton*. On the lateral aspect of the scapula, a shallow depression was interpreted as the origin of the *procoracohumeralis* ('scapulohumeralis') in captorhinids (Holmes, 1977), and we observed a similar depression in *Archeria* (sh, Fig. 8J). A ridge on the external anterior edge of the coracoid in captorhinids was interpreted as the dorsal extent of the *supracoracoideus* (Holmes, 1977), and in *Archeria* a gap between the coracoid plate and clavicle was interpreted as this muscle's passage to the humerus (black arrow, Fig. 8K) (Romer, 1957). On the posterodorsal corner of the coracoid in captorhinids, a slight swelling was interpreted as the origin of the *triceps coracoideus* (Holmes, 1977). In *Eoherpeton*, the posteroventral continuation of the coracoid plate was interpreted as the origin of the *coracobrachialis* (Smithson, 1985), in agreement with Romer (1922), who described a small distinct surface on the posterior edge of the coracoid as the origin of the *coracobrachialis longus* in many early tetrapods. In *Archeria*, a concavity bounded anteriorly by a ridge occupies this region (cb, Fig. 8J) (Romer, 1957). In captorhinids, a very shallow depression on the scapula and suprascapula was interpreted as the scapular origin of the *deltoideus*, and a posterior flange on the ventral portion of the clavicular stem as the origin of the *deltoideus clavicularis*, a derivative of the *procoracohumeralis* (Holmes, 1977). In *Eoherpeton*, striations are described on the dorsal plate and stem of the clavicle, distinct from the dermal ornament on its external surface, but the study did not speculate about their significance (Smithson, 1985). Striations are described on the external aspect of the clavicle in *Archeria*, but not on its ascending process (str, Fig. 8J) (Romer, 1957).

## (2) Humerus

### (a) *Onychodontids and dipnomorphs*

As in extant sarcopterygian fish, the humerus of onychodontids and dipnomorphs bears dorsal and ventral processes which are thought to be homologous with the tetrapod ectepicondyle and entepicondyle, respectively (Ahlberg, 1989; Friedman, Coates & Anderson, 2007). A dorsal process is present on the humerus of the fossil lungfish *Pentlandia* ('axial process'; Jude *et al.*, 2014), but the ventral aspect of this bone is not exposed. The humerus of the earlier diverging dipnomorph *Glyptolepis* has a very large ventral process and a smaller dorsal process (vp and dp, respectively; Fig. 9A, B). Several features of the humerus of *Onychodus* have been suggested as attachments





(‘supinator’) (fig. 5A of Rackoff, 1980), but because the supinator ridge is closely associated with the deltoid process in many other tetrapodomorph fish (e.g. *Barameda*, *Rhizodus*, *Gogonasmus*, *Eusthenopteron*) we consider it more likely that the *brachioradialis* originated from the deltoid process. On the ventral aspect of the bone, the ventral (‘humeral’) ridge and entepicondyle, confluent in *Gogonasmus*, *Eusthenopteron* (Fig. 9F) and *Tiktaalik*, are separate in *Panderichthys* (Boisvert, 2009). In *Sterropterygion*, the ventral humeral ridge is divided into a series of large, distinct processes interpreted as the insertions for ‘ventral flexor musculature’ (Thompson, 1972) or origins for ‘ulnar flexor musculature’ (Rackoff, 1980) and the *pectoralis*. Thompson (1972) argued that *Sterropterygion* was capable of tetrapod-like, terrestrial locomotion and inferred attachments for other tetrapod muscles, such as the *coracobrachialis*, *subcoracoscapularis*, *triceps humeralis medialis*, and *supracoracoideus* (Rackoff, 1980). However, because *Sterropterygion* retains lepidotrichia and because the aforementioned reconstructed muscles are not associated with osteological correlates, we consider it more likely that any specializations of the pectoral appendicular muscles were related to aquatic locomotion. Two additional correlates were identified in *Eusthenopteron* but not in the other tetrapodomorph fish (and so should be taken with caution): a large, shallow recess on the proximal ventral humerus and an ill-defined ridge between the proximal extent of the humeral ridge and the deltoid-supinator ridge, interpreted as the insertions of the *coracobrachialis* and *supracoracoideus*, respectively (cb? and scc?, Fig. 9E, F) (Andrews & Westoll, 1970a).

Controversies surround the presence and identification of several morphological characteristics of tetrapodomorph fish humeri, including the *pectoralis* process, latissimus dorsi process, and differentiation of individual deltoid and supinator processes. The proximal, preaxial extreme of the ventral humeral ridge has been identified as the *pectoralis* insertion in *Eusthenopteron* (Andrews & Westoll, 1970a), *Panderichthys* (Vorobyeva, 2000) and the Catskill humerus (ANSP 21350 – a stem tetrapod) (fig. 2 of Shubin *et al.*, 2004). However, based on comparison of humeri from different ontogenetic stages in the stem tetrapod *Ichthyostega*, Callier *et al.* (2009) argued convincingly that the *pectoralis* process first appeared in the middle of the ventral humeral ridge. Therefore, *Panderichthys* and *Tiktaalik* are interpreted as lacking a pectoral process, while that of the Catskill humerus is weakly developed, a position followed by Ahlberg (2011). This means that the ‘pectoralis process’ in *Rhizodus*, *Strepsodus* (Andrews & Westoll, 1970b; Jeffery, 2001) (black arrow, Fig. 9D), *Sauripterus* (Davis *et al.*, 2004) and *Sterropterygion* (Rackoff, 1980), located at the preaxial end of the ventral humeral ridge, was probably misidentified (i.e. it merely represents part of a continuous ridge).

The prevalence of a latissimus dorsi process among tetrapodomorph fish is the subject of some debate. It is thought to be present either as a process or as a series of diagonal ridges in *Panderichthys* and *Tiktaalik* (Vorobyeva, 2000; Boisvert, 2009; Ahlberg, 2011) but absent in *Gogonasmus*

(Boisvert, 2009) and *Eusthenopteron* (Andrews & Westoll, 1970a). In *Strepsodus*, Andrews & Westoll (1970a,b) described a process on the dorsal postaxial surface of the humerus and argued that it is homologous with the latissimus dorsi process of tetrapods, also suggesting that *Rhizodus* probably had a similar process. Vorobyeva (2000) also describes a latissimus dorsi process in these two taxa. However, Jeffery (2001), who examined additional specimens, contended that neither fish has a latissimus dorsi process. In *Strepsodus*, the two structures previously identified as possible latissimus dorsi processes are, according to Jeffery (2001), either part of the ventral humeral ridge or result from damage to the specimen (white and black arrows in Fig. 9C, respectively). Young *et al.* (1992) identified a latissimus dorsi process on the humerus of the tetrapodomorph fish *Notorhizodon*, but Johanson & Ahlberg (2001) argued that, not only did the humerus belong to a different fossil (which they named *Aztecia mahalae*), but the ‘latissimus dorsi process’ of Young *et al.* (1992) is actually the ectepicondyle, and that the previously identified ectepicondyle is instead a separate bone. Finally, Parker *et al.* (2005) suggested that this process in *Aztecia* might instead represent the deltoid and supinator areas of the dorsal ridge, similar to *Strepsodus*; however, the study also stated that damage in this region of the humerus may be too great to permit accurate interpretation. Because none of the processes identified in these taxa resemble the oblique ridges identified by Ahlberg (2011) as *latissimus dorsi* attachments in *Tiktaalik* and *Panderichthys*, and because there is no intermediate condition known, we consider this feature (*latissimus dorsi* insertion) to be on the dorsal process or ridge (i.e. no separate insertion) in *Rhizodus*, *Strepsodus*, and *Aztecia*.

Another controversy regarding tetrapodomorph fish humeri involves the differentiation of separate deltoid and supinator processes from the dorsal ridge. This character has been proposed as a synapomorphy or symplesiomorphy of rhizodonts, ‘osteolepiforms’, and tetrapods (Ahlberg, 1989), but some studies dispute its presence in the rhizodonts *Rhizodus* and *Barameda* and the ‘osteolepiforms’ *Gogonasmus* and *Eusthenopteron* (‘osteolepiforms’ is a paraphyletic superorder containing taxa that are closer to tetrapods than rhizodonts but not as close as *Panderichthys*; Ahlberg & Johanson, 1998). Andrews & Westoll (1970b) identified separate processes in *Rhizodus*, but this area of the bone in the specimen they examined (PMG 297) is broken and it is difficult to verify their presence. Vorobyeva (2000) identified a separate ‘supinator attachment’ process in *Rhizodus* in a different location: distal to the dorsal ridge. Jeffery (2001) re-examined the specimens, including a second, more-complete specimen of *Rhizodus* (NMS G 1972.434c), and concluded that the processes that make up the dorsal ridge are not clearly differentiated and that the ‘supinator attachment’ of Vorobyeva (2000) in *Strepsodus* (grey arrow, Fig. 9C) is an artefact of crushing damage to the dorsal ridge. In their re-description of *Barameda*, Garvey *et al.* (2005) challenged Jeffery’s (2001) assertion, noting that a depression similar to the ‘supinator attachment’ of Vorobyeva (2000) – which they call the ‘ectepicondylar depression’ after Long (1989) – is present not

only in *Strepsodus* but also in *Barameda*, *Sauripterus* and *Rhizodus* and therefore is unlikely to be the result of crushing. In *Barameda*, this depression has striations interpreted as muscle attachment scars (Garvey *et al.*, 2005). Jeffery (2001) also suggested that the deltoid and supinator processes identified by Long (1989) in *Barameda* may be part of a continuous dorsal ridge, as in *Rhizodus*, and Garvey *et al.* (2005) do not disagree with this position, noting that continuous ridges are present in *Aztecia* and *Sauripterus*, although their orientation is somewhat different. In *Gogonasmus*, Holland (2013) described a deltoid process that was ‘rounded, moderate in size, and is marked with scars for muscle attachment’ and, distally, a ‘large supinator process, which is pointed and marked with a small circular area of unfinished bone’ (p. 156). However, Boisvert (2009) labeled this process as the ectepicondyle (their fig. 4A) and stated that the deltoid and supinator processes in *Gogonasmus* are part of a continuous flange (p. 303). Indeed, the ‘supinator process’ of Holland (2013) resembles the ectepicondyle in other tetrapodomorph fish in that it is located at the extreme distal end of the bone at the end of a thick, longitudinal ridge. Furthermore, Andrews & Westoll (1970a) identified ‘incompletely separated’ supinator and deltoid processes in *Eusthenopteron* (p. 240) (arrows, Fig. 9E), whereas Boisvert (2009) considered these processes, like those of *Gogonasmus* and *Tiktaalik*, to be part of a continuous flange. For the purposes of muscle reconstruction, this disagreement is irrelevant: neither interpretation would clearly indicate the presence of separate muscles. Therefore, we consider this character state (*deltoideus* and *brachioradialis* humeral attachments) in *Barameda*, *Rhizodus*, *Gogonasmus*, and *Eusthenopteron* to be uncertain: either deltoid-supinator ridge or separate deltoid and supinator processes.

### (c) Stem tetrapods

Morphological features of the humerus of the stem tetrapod *Acanthostega* were described in detail by Coates (1996). The humerus shares many of the characters described above in *Panderichthys* and *Tiktaalik*, including ectepicondyle, latissimus dorsi process, humeral ridge, and entepicondyle, plus additional features shared with other stem tetrapods such as *Ichthyostega*, *Tulerpeton*, and *Greerpeton* (Coates, 1996) (Fig. 9G, H), described in the following paragraph. Jarvik (1980, 1996) described many processes on the humerus of *Ichthyostega* but only attempted to identify a few of them (ectepicondyle, dorsal ridge); moreover, the identification of these structures was challenged by Panchen (1985), and most subsequent studies, including Coates (1996) and Callier *et al.* (2009), have followed the interpretations of the latter.

On the proximal dorsal aspect of the humerus of *Acanthostega* is the *latissimus dorsi* attachment (ldp, Fig. 9G) (Coates, 1996), which was also identified in all but three of the descriptions of the other stem tetrapods we reviewed. As in the tetrapodomorph fish *Panderichthys* and *Tiktaalik*, this attachment is represented by one or more ridges in *Acanthostega* and the Catskill humerus, whereas in *Ichthyostega* it is probably represented by a process confluent with the ectepicondyle (‘process 1’ of Jarvik, 1996; Ahlberg, 2011). In

the remaining taxa we surveyed, the process is distinct and often spike-like, as in *Baphetes* (Milner & Lindsay, 1998) and *Pederpes* (ldp, Fig. 9I) (Clack & Finney, 2005). Proximal and anterior to the *latissimus dorsi* attachment is a depression where the *procoracohumeralis* is thought to have inserted (shd, Fig. 9G;) (‘scapulohumeralis-like muscle’; Coates, 1996). In other stem tetrapods (e.g. Catskill humerus, *Ichthyostega*, *Acanthostega*), this muscle attachment is usually described as a shallow concavity (e.g. Shubin *et al.*, 2004) or as a rugose ridge posterior to a concavity (Ahlberg, 2011). On the posterior edge of the humerus of *Acanthostega* just proximal to the beginning of the ectepicondyle is a process with scarring on its ventral surface, interpreted as the insertion of the *subcoracoscapularis* (scs, Fig. 9H) (Coates, 1996). Coates (1996) considered this process to be homologous with ‘process 2’ of *Ichthyostega* (Jarvik, 1996). A recess and/or process is present in this location in other stem tetrapods [e.g. *Baphetes* (Milner & Lindsay, 1998), Catskill humerus (Shubin *et al.*, 2004)], and when both are present, as in *Crassigyrinus*, they may mark insertions of separate *subcoracoideus* and *subscapularis* muscles (Panchen, 1985). On the anterior edge of the humerus of *Acanthostega*, about two-thirds of the way along its length, is the convex supinator process (sp, Fig. 9G) (Coates, 1996). In many stem tetrapods, the supinator process extends as a ridge toward the ectepicondyle (Ahlberg, 2011), which makes up the posterior distal portion of the bone. The identity of the semi-horizontal ridge on the dorsal aspect of the humerus of *Ichthyostega* (cr. 1–5 in fig. 45A, D of Jarvik, 1996) has been debated; while Ahlberg (2011) homologized it with the supinator ridge of other tetrapod humeri, Bishop (2014) argued that it might represent part of the *latissimus dorsi* attachment (‘latissimus-deltoid ridge’). If the latter interpretation is correct, *Ichthyostega* lacks a supinator ridge. However, we follow the former interpretation because, according to our observations, this region of the humerus in *Ichthyostega* is very similar to that of the other stem tetrapods we surveyed.

The deltopectoral crest occupies the anterior portion of the ventral aspect of the humerus of *Acanthostega* (dpc, Fig. 9H) (Coates, 1996). The main difference between the humeri of *Ichthyostega* and *Acanthostega* is that in the former taxon (and the Catskill humerus), the pectoralis process and deltoid process are separated by the prepectoral space; thus the pectoralis process is confluent with the ventral humeral ridge rather than being united with the deltoid process to produce the deltopectoral crest (Ahlberg, 2011). This condition reflects the evolutionary origin of the *pectoralis* as part of a larger ventral muscle mass and the continuation of a general trend toward breakup of large muscle sheets into individual muscles across the fins-to-limbs transition (Callier *et al.*, 2009). In *Baphetes*, a slight ridge on the ventromedial aspect of the deltopectoral crest was interpreted as the origin of the *humeroantebrachialis* (‘brachialis’; Milner & Lindsay, 1998), as were scars in the same region in *Crassigyrinus* and *Ossinodus* (Smithson, 1985; Bishop, 2014). The proximal ventral surface of the humerus in *Acanthostega* is divided into two distinct regions, a smooth anterior region and a rough,

concave posterior region, thought to mark the insertions of the *supracoracoideus* anteriorly and *coracobrachialis* posteriorly (scc and cb, Fig. 9H) (Coates, 1996). A similar configuration is described in other stem tetrapods such as *Baphetes* (Milner & Lindsay, 1998), *Crassigyrinus* and *Ichthyostega* (Panchen, 1985), *Greerpeton* (Godfrey, 1989), and *Tulerpeton* (Lebedev & Coates, 1995).

#### (d) Crown tetrapods

The humerus of *Eryops* has many well-developed processes for muscle attachment. The deltopectoral crest is separated into deltoid and pectoral crests for insertion of the respective muscles (dep and pec, Fig. 9K, L) (Miner, 1925). There is also a distinct 'supinator process' (sp, Fig. 9K, L) thought to mark the origin of the 'supinator longus' (*brachioradialis*; fused with the *extensor antebrachii et carpi radialis* in *Salamandra* but present as a separate muscle in some salamanders; Diogo & Abdala, 2010) and two distinct facets that were interpreted as origins of the *triceps humeralis medialis* and *lateralis* (tm and tl, respectively; Fig. 9K). The entepicondyle (en, Fig. 9K, L) is greatly expanded; its anterior margin was thought to have provided the insertion for the *coracobrachialis longus* and *brevis* and a ridge on its surface the origin of the *flexor antebrachii et carpi radialis* (Miner, 1925). There is also a distinct latissimus dorsi process (ldp, Fig. 9K). In addition, in *Eryops*, Pawley & Warren (2006) identified a ridge [proximal humeral ridge (phr), Fig. 9L] on the proximal anterior surface that may have separated the origins of the *procoracohumeralis* and *subcoracoscapularis*. Thus, among the muscles that attach to the humerus in *Salamandra*, only the *brachialis* and *supracoracoideus* lack osteological correlates in *Eryops*.

In all three fossil amniotes and stem amniotes we surveyed, correlates were identified for the insertions of the *coracobrachialis*, *supracoracoideus*, *latissimus dorsi*, and *subcoracoscapularis*, and individual scars on the deltopectoral crest were identified as insertions of the *pectoralis* and *deltoideus*. The insertion of the *coracobrachialis* on the proximal ventral humerus is indicated by a concavity in *Eoherpeton* and a ridge marking its anterior extent in *Archeria* (cbr, Fig. 9N) (Romer, 1957; Smithson, 1985). In captorhinids, a similar concavity was identified as the insertion of the *coracobrachialis brevis*, and an additional correlate, a ridge on the proximal edge of the entepicondyle, was identified as the insertion of the *coracobrachialis longus* (Holmes, 1977). Also on the proximal ventral surface, the *supracoracoideus* insertion is marked by slight rugosities in *Archeria* (scc, Fig. 9N) and a tuberosity in *Eoherpeton* (Romer, 1957; Smithson, 1985). In captorhinids, a scar on the deltopectoral crest was interpreted as the insertion of the *supracoracoideus* (Holmes, 1977). On the proximal dorsal humerus is a small tubercle (in *Eoherpeton*) or ridge (in *Archeria* and captorhinids) (ldp, Fig. 9M), identified as the insertion of the *latissimus dorsi* (Romer, 1957; Holmes, 1977; Smithson, 1985). On the posterodorsal aspect of the head of the humerus, the insertion of the *subcoracoscapularis* is identified as a tubercle in *Archeria* (scs, Fig. 9M), a depression in *Eoherpeton*, and a raised area of bone in captorhinids (Romer, 1957; Holmes, 1977; Smithson, 1985).

In addition, small tubercles associated with the origin of the *brachioradialis* ('supinator') were identified in *Eoherpeton* and captorhinids (Holmes, 1977; Smithson, 1985), and ridges on the head of the humerus for the insertion of the *procoracohumeralis* in *Archeria* [scapulohumeral muscle (shd), Fig. 9M] and captorhinids (Romer, 1957; Holmes, 1977). In captorhinids, a faint ridge on the dorsolateral humerus was interpreted as having separated the origins of the *triceps humeralis lateralis* and *medialis* (Holmes, 1977). The origin of the *humeroantebrachialis* is marked by a scar on the distal surface of the deltopectoral crest in *Eoherpeton* (Smithson, 1985) and the proximal ventral portion of the anterior flange that extends from this process to the entepicondyle in *Archeria* (sp, Fig. 9M) (Romer, 1957). Finally, in *Archeria* there is a distinct process projecting from the entepicondyle interpreted as part of the origin of the forearm flexor musculature (ff, Fig. 9N) (Romer, 1957).

### (3) Radius/ulna

The morphology of the radius and ulna varies widely among sarcopterygian fish, and we were not able to trace homologous correlates on these bones. However, distinctive processes appeared in stem tetrapods, and some persist in extant lizards and salamanders.

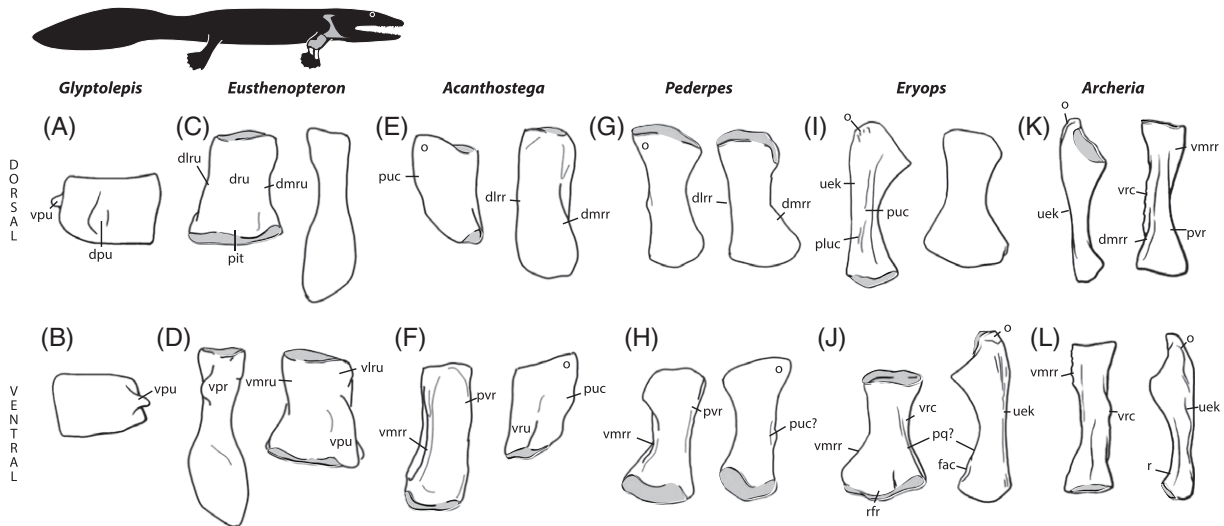
#### (a) Onychodontids and dipnomorphs

In dipnomorphs, the ulna resembles the humerus, with similar dorsal and ventral processes, and only in *Pentlandia* is the radius present as a separate bone (Jude *et al.*, 2014). The ulna of *Pentlandia* carries a dorsal process, but its ventral surface was not exposed; the radius does not have a dorsal process (Jude *et al.*, 2014). The ulna of *Glyptolepis* has both dorsal and ventral processes (dpu and vpu, Fig. 10A, B) (Ahlberg, 1989).

#### (b) Tetrapodomorph fish

The ulna of tetrapodomorph fish is broader distally than proximally and lacks an olecranon process (Ahlberg, 2011). The five ulnae we reviewed have little else in common in terms of bony features. In *Barameda* and *Strepsodus*, grooves separate the two distal facets and extend along the dorsal and ventral faces (Garvey *et al.*, 2005; Parker *et al.*, 2005). In *Rhizodopsis*, the dorsal surface is smooth with a small pit at the distal end; the ulna lacks a postaxial process, and the ventral surface is unknown (Andrews & Westoll, 1970b). In *Gogonassus*, a concave, circular region of unfinished bone with a distal groove is described on the proximal dorsal surface (Holland, 2013). In *Eusthenopteron*, a strongly developed ventral postaxial process (vpu, Fig. 10D) was interpreted as a muscle insertion site (Andrews & Westoll, 1970a). Additional longitudinal ridges are present as well [Fig. 10C, D: dorsal (dru), dorsomesial (dmru), dorsolateral (dlru), ventromesial (vmru), and ventrolateral (vlru), which culminates in the ventral process], as well as a small pit on the distal dorsal surface (Andrews & Westoll, 1970a).





**Fig. 10.** Right radius and ulna of the dipnomorph *Glyptolepis* (A, B), the tetrapodomorph fish *Eusthenopteron* (C, D), the stem tetrapods *Acanthostega* (E, F) and *Pederpes* (G, H), the temnospondyl *Eryops* (I, J), and the embolomere *Archeria* (K, L) (modified from Ahlberg, 1989; Andrews & Westoll, 1970a; Coates, 1996; Clack & Finney, 2005; Pawley & Warren, 2006; Romer, 1957). Articular surfaces shaded in grey. Abbreviations: dorsal process of ulna (dpu), dorsal ridge of ulna (dru), dorsolateral ridge of radius (dlrr), dorsolateral ridge of ulna (dlru), dorsomesial ridge of radius (dmrr), dorsomesial ridge of ulna (dmru), facet (fac), olecranon process (o), posterior ulnar crest (puc), posterolateral ulnar crest (pluc), *pronator quadratus* attachments (pq), proximoventral ridge (pvr), ridge (r), radial flexor ridge (rfr), ulnar extensor keel (uek), ventromesial ridge of radius (vmrr), ventromesial ridge of ulna (vmru), ventral process of radius (vpr), ventral process of ulna (vpu), ventral radial crest (vrc), ventral ridge of ulna (vru), ventrolateral ridge of ulna (vlru). Silhouette at top left shows configuration of pectoral girdle and limb bones (radius and ulna in white) in *Acanthostega gunnari*.

In *Panderichthys*, several longitudinal grooves and ridges are present on both the dorsal and ventral aspects of the ulna (Vorobyeva, 2000; Boisvert *et al.*, 2008). On the ulna of *Tiktaalik*, there is a low ridge on the dorsal aspect and several processes and rugosities on the ventral aspect, interpreted as possible muscle attachments (Shubin *et al.*, 2006).

Likewise, several tetrapodomorph fish have scars or processes on the radius, but they are difficult to homologize. In *Sauripterus* there are several longitudinal ridges on the ventral radius, interpreted as attachments for ‘ventral flexor and rotator musculature’ (Davis *et al.*, 2004, p. 34). No features are described on the radius of *Barameda* (Garvey *et al.*, 2005) or *Rhizodopsis* (Andrews & Westoll, 1970b). The proximal portion of the radius in *Eusthenopteron* and *Gogonasus* has small processes, located on the ventral and preaxial aspects, respectively (vpr, Fig. 10D) (Andrews & Westoll, 1970a; Holland, 2013). In *Panderichthys* and *Tiktaalik*, there is a crest along the preaxial edge (Shubin *et al.*, 2006; Boisvert *et al.*, 2008).

### (c) Stem tetrapods

Tetrapod ulnae are characterized by an ossified olecranon process and a confluent posterior flange or ridge (‘extensor crest’) (Ahlberg, 2011). These two features are present in all the taxa we surveyed for which the ulna was preserved, including *Ichthyostega*, *Acanthostega*, *Pederpes*, and *Tulerpeton* (o and puc, Fig. 10E–H). In *Crassigyrinus*, the presumed ulna does not appear to have an ossified olecranon process or posterior ridge (Panchen, 1985). In *Pederpes*,

the posterior ridge is separated from the small olecranon process and located slightly distal to the middle of the shaft (puc?, Fig. 10H) (Clack & Finney, 2005). In *Ichthyostega*, the olecranon process and posterior keel are extremely well-developed, and the former is bifurcated (Jarvik, 1996). Additional ridges on the ventral and radial aspects of the ulna were described in *Greererpeton* (Godfrey, 1989) and the former was figured but not described in *Acanthostega* (Coates, 1996) and was observed by us (vru, Fig. 10F; arrow 3, Fig. S1D).

The radii of *Ossinodus*, *Pederpes*, *Acanthostega*, *Greererpeton*, and *Baphetes* bear four longitudinal ridges: dorsomesial, dorsolateral, proximoventral, and ventral median (*sensu* Bishop, 2014), which give them a roughly rectangular shape (Fig. 10E–H). The ventral median ridge (vmrr, Fig. 10F, H) often has obvious muscle scars and has been interpreted as the insertion of the *humeroantibrachialis* (‘brachialis’; Bishop, 2014). In *Ossinodus*, the dorsomesial ridge was interpreted as the insertion of the *brachioradialis* (‘supinator longus’) and the proximoventral ridge as the insertion of the *extensor carpi radialis* (similar ridges are present in *Acanthostega* and *Pederpes*: dmrr and pvr, Fig. 10E–H), but there is no break in the muscle scarring between the two ridges, so the insertions may not be separate (Bishop, 2014). The prominent ventral radial crest in *Ossinodus* does not have muscle scarring, but an area of scarring on the face of the radius between this ridge and the ventral median ridge was interpreted as the insertion of the *flexor antibrachii et carpi radialis* (Bishop, 2014). This interpretation echoes Godfrey’s (1989) suggestion that the two mesial ridges on the radius of *Greererpeton* mark the separation between the extensor and flexor muscle masses.



Anterior and medial radial ridges are described in *Ichthyostega*, in addition to a longitudinal groove on the posterolateral side that merges into a concave triangular area on the proximal end of the bone (Jarvik, 1996).

(d) *Crown tetrapods*

Many of the same skeletal correlates present in stem tetrapods were also present, and interpreted similarly, in the extinct crown tetrapods we surveyed. On the ulna of various crown tetrapods, the olecranon process, posterior ulnar crest, and ventral ridge of ulna were identified as the insertions of the *triceps*, the boundary between the dorsal and ventral forearm musculature, and the medial boundary of the ulnar flexor musculature, respectively. On the radius, ventromedial and ventrolateral ridges and a ventral radial crest were identified as the insertion of the *humeroantebrachialis*, the division between the flexor and extensor musculature, and the insertion of the *brachioradialis*, respectively (see below for details and citations for individual taxa).

The ulna of *Eryops* shows an ulnar extensor keel distal to the olecranon process, posterior ulnar crest, and posterolateral ulnar crest (uek, puc, and pluc, Fig. 10I) (Pawley & Warren, 2006). A facet on the radial face of the distal ulna (fac, Fig. 10J) was interpreted as the origin of the *flexor accessorius medialis* and/or *lateralis* ('palmaris profundus dorsalis') or part of the *pronator quadratus* (Miner, 1925). Opposing ridges on the inner edges of the radius and ulna were suggested as the origin and insertion of the *pronator quadratus* (pq?, Fig. 10J) (Miner, 1925). On the radius a ventromesial radial ridge, radial flexor ridge, and ventral radial crest are evident (vmrr, rfr, and vrc, Fig. 10J; Pawley & Warren, 2006).

In captorhinids and *Archeria*, the well-developed olecranon process tapers to a thin ridge that extends along the postaxial aspect of the ulna (o and uek, Fig. 10K, L) (Romer, 1957; Holmes, 1977), and in captorhinids this ridge was interpreted as a possible boundary between the *epitrochleoanconeus* and the *anconeus quartus*, a derivative of the *extensor carpi ulnaris*. The ventral surface of the lateral portion of the ulna in captorhinids is roughened, suggesting an insertion area of the *epitrochleoanconeus* (Holmes, 1977). The ventral surface of the ulna in *Archeria* is concave and a faint ridge (r, Fig. 10L) separates the ventral surface from the medial (radial) surface of the bone (Romer, 1957), creating a distal facet similar to that of *Eryops*.

In *Archeria*, a rugosity on the ventral median ridge of the radius (vmrr, Fig. 10K, L) was interpreted as the insertion of the *humeroantebrachialis* ('humeroradialis'; Romer, 1957) – as in *Ossinodus* – and *biceps*, if present. The remainder of this ridge and a matching lateral ridge were interpreted as marking boundaries between the extensor and flexor muscle groups (Romer, 1957). No similar ridges were described in captorhinids. Ventral longitudinal radial ridges are present in both taxa [ventral radial crest (vrc), Fig. 10L], possibly homologous with the 'distal ventral keel' in *Eryops* (Romer, 1957) – presumably the 'radial flexor ridge' of Pawley & Warren (2006). In captorhinids, the ventral process was

interpreted as the insertion of the *brachioradialis* ('supinator longus').

#### IV. PROPOSED HOMOLOGOUS OSTEOLOGICAL CORRELATES IN THE SARCOPTERYGIAN LINEAGE: FROM FISH TO TETRAPODS

Following the muscle homology hypotheses of Diogo *et al.* (2016) (Table 2; Fig. 5) and a survey of osteological correlates of muscle attachment in extant and fossil sarcopterygians (Sections II and III), we identified potential homologies between osteological correlates described in the fish and tetrapod lineages.

##### (1) Pectoral girdle

Because much of the pectoral girdle in salamanders and many of their ancestors is unossified, it is difficult to trace osteological correlates backwards through the tetrapod lineage. Only a few muscles leave conspicuous osteological correlates on the pectoral girdle in either salamanders or lizards (one and two out of 10, respectively), so the identification of correlates on the pectoral girdles of fossil tetrapodomorph fish and stem tetrapods is somewhat speculative. However, because the homologies of these muscles are well established based on embryonic origin and phylogenetic distribution among extant taxa, and given that the areas of origin of the muscles appear to be fairly conserved between lizards and salamanders (Fig. 7), and enough fossils exist with well-developed osteological correlates, it is possible to trace the general, relative (but not specific or precise) attachments of many of these muscles with reasonable confidence to the last common ancestor (LCA) of crown tetrapods. Miner (1925) took this approach to reconstruct the pectoral musculature of the temnospondyl amphibian *Eryops*. We revise and expand on this reconstruction here by combining it with data from sarcopterygian fish and additional tetrapods, both extant and extinct.

We identified three possible homologous osteological correlates between fish and tetrapods on the pectoral girdle. The longitudinal ridge (Fig. 4A) on the cleithrum and clavicle of *Neoceratodus* marks the origin of the proximal portion of the *abductor superficialis* (Fig. 6B). The ventral cleithral ridge (Fig. 4D) was interpreted as the anterior extent of the origin of the *pectoralis* in the rhizodontid fishes *Sauripterus* (Davis *et al.*, 2004), *Gogonasmus* (Boisvert, 2009), and *Eusthenopteron* (Andrews & Westoll, 1970a). However, the cleithral attachment of the *pectoralis* seems to have been lost in later tetrapods, and the cleithrum itself eventually disappeared. Because the *pectoralis* and *abductor superficialis* are homologous according to the hypotheses in Table 2, the ventral cleithral ridge and longitudinal ridge are probably homologous as well.

The deeper muscle *adductor profundus* originates from the dorsal, scapular part of the scapulocoracoid just above the glenoid in both *Latimeria* and *Neoceratodus*, its attachment in

the latter fish being marked by a distinct facet (Fig. 6A). A seemingly homologous shallow fossa on the lateral face of the scapulocoracoid anterodorsal to the glenoid has been identified as the origin for ‘scapulohumeral muscles’ in several stem tetrapods, including *Hynierpeton* (Daeschler *et al.*, 1994) and *Ossinodus* (Bishop, 2014) and in captorhinids (Holmes, 1977).

The ridge above the glenoid in *Latimeria* marks the origin of *pronator 1* (Fig. 6G). In *Neoceratodus*, this muscle is either absent or part of the *adductor profundus*, which also originates just dorsal to the glenoid (Fig. 6A). In *Salamandra* and *Iguana*, the homologous muscle *subcoracoscapularis* originates from the inner surfaces of the procoracoid and coracoid, respectively, but has no osteological correlate (Miner, 1925; Francis, 1934) (Fig. 7A, G). However, a fossa or rugose area on the posterior border of the scapulocoracoid bounded anteriorly by a ridge (tr, Fig. 8H, J) has been identified as the origin of the *subcoracoscapularis* (‘subscapularis’) in a number of stem tetrapods and extinct crown tetrapods, including captorhinids (Holmes, 1977), *Archeria* (Romer, 1957), *Ossinodus* (Bishop, 2014), and *Tulerpeton* (Lebedev & Coates, 1995). In *Eusthenopteron*, a small mark on the posterior border of the scapulocoracoid was suggested as a possible origin for this muscle (Andrews & Westoll, 1970a), and this location is topologically consistent with the previously mentioned fossa, being adjacent to the glenoid near the junction of the scapular and coracoid regions.

## (2) Humerus

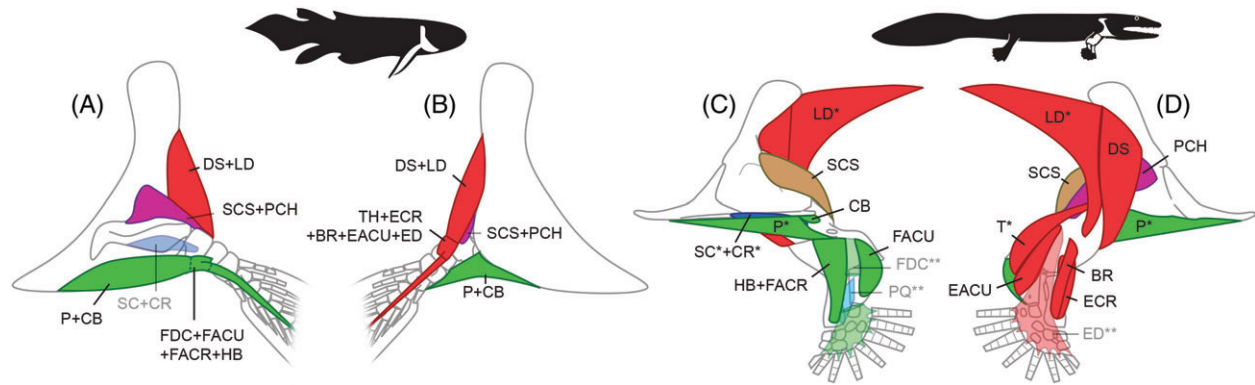
On the humerus, two osteological correlates in sarcopterygian fish appear to be homologous with multiple correlates in tetrapods, reflecting the breakup of a few large muscles into numerous smaller ones. The ventral process (or ‘postaxial process’) in lobe-finned fish is thought to be homologous with the entepicondyle and ventral humeral ridge of tetrapods, and its presence is considered to be a sarcopterygian synapomorphy (Andrews & Westoll, 1970a; Ahlberg, 1989; Jeffery, 2001; Friedman *et al.*, 2007). In tetrapodomorph fish such as *Strepsodus*, *Sauripterus*, *Gogonasmus*, and *Eusthenopteron*, the entepicondyle is continuous with the ventral humeral ridge (‘oblique ventral ridge’), part of which forms the pectoralis insertion (hr, Fig. 9D, F) (Davis *et al.*, 2004; Boisvert, 2009; Holland, 2013). The ventral process in coelacanth serves as the attachment for the most proximal of the tendinous intersections that divide the *abductor superficialis*. Thus, in both coelacanth and tetrapodomorph fish the ventral process and its derivatives form the insertion for homologous superficial stylopodial flexors and the origin for homologous superficial zeugopodial and autopodial flexors. The stylopodial flexors are the proximal portion of the *abductor superficialis* in coelacanth (Fig. 5A, B) and the *pectoralis*, and *coracobrachialis longus* and *brevis* in tetrapods (Fig. 5E, F). The zeugopodial and autopodial flexors are the middle portion of the *abductor superficialis* in coelacanth, and the *flexor digitorum*, *flexor antebrachii et carpi ulnaris*, and possibly the *flexor antebrachii et carpi radialis* in tetrapods.

The dorsal process in sarcopterygian fish is thought to be homologous with the ectepicondyle, which subsequently gave rise to the deltoid and supinator processes (Ahlberg, 1989). The latissimus dorsi process first appeared at the proximal border of the ectepicondyle (in *Tiktaalik*; Boisvert, 2009), suggesting that it represents an attachment for a derivative of the same muscle mass. In coelacanth, the superficial dorsal muscles that cross the shoulder and elbow (*adductor superficialis*) are attached to the dorsal process (Fig. 6I). Thus, mirroring the arrangement on the ventral side, the dorsal ridge and its derivatives form the insertion for homologous superficial stylopodial extensors [proximal portion of the *adductor superficialis* in coelacanth; *deltoides* and *latissimus dorsi* in tetrapods (Figs. 6G, H and 7I, J)] and the origin for homologous superficial zeugopodial extensors (middle portion of *adductor superficialis* in coelacanth; *extensor antebrachii et carpi radialis* + *brachioradialis*, *extensor digitorum*, and *triceps humeralis* in tetrapods).

## (3) Ulna

The ventral and dorsal processes of the ulna in *Latimeria* are similar to those of the humerus: they have similar shapes and orientations, and they also form the attachments for tendinous intersections dividing the superficial ventral and dorsal musculature, respectively (Fig. 6K, L). The middle portion of the *adductor superficialis* in *Latimeria* ends at its attachment to the dorsal process of the ulna. It is tempting to homologize the dorsal process with the olecranon process and posterior ulnar keel in tetrapods, where the *triceps* and *extensor antebrachii et carpi ulnaris* (both derivatives of the superficial dorsal musculature) are thought to have inserted. However, no similar process exists in tetrapodomorph fish such as *Eusthenopteron*. Instead, the superficial dorsal musculature probably inserted on the proximal end of the bone without leaving a mark (Andrews & Westoll, 1970a); this region is distinguished by an area of unfinished bone in the tetrapodomorph fish *Gogonasmus* (Holland, 2013).

The ventral process of the ulna, like that of the humerus, is more pronounced than the dorsal process in *Latimeria*, *Neoceratodus*, and the fossil lungfish *Glyptolepis* (Ahlberg, 1989). In *Latimeria*, the ventral process forms the attachment for the tendinous intersection that divides the middle and distal portions of the *abductor superficialis* (Fig. 6L). It is also present in the tetrapodomorph *Eusthenopteron* (vpu, Fig. 10D) and was described as the serial homologue of the ventral process of the humerus (Andrews & Westoll, 1970a), implying that it is homologous with the ventral process of the ulna in extant lobe-finned fish. Ridges on the ventral ulna are present in several stem tetrapods and in *Eryops*. However, the ventral process probably is not homologous with the ventral ulnar ridge of salamanders because this feature is located in the region of attachment of deep muscles (Fig. 7F) that are not proposed to be homologous with any part of the superficial musculature.



**Fig. 11.** Reconstructions of muscle anatomy in the right pectoral appendage of the hypothetical last common ancestor (LCA) of tetrapodomorphs (A, B) and of the LCA of tetrapods (C, D). Medial (A, C) and lateral (B, D) views; silhouettes show orientation of B and D. \* indicates area of origin uncertain; \*\*area of insertion uncertain. Colours correspond to Fig. 5. Muscles in grey text are inferred to be present based on homology but are not associated with osteological correlates. Abbreviations: *brachioradialis* (BR), *coracobrachialis* (CB), *coracoradialis* (CR), *deltoideus scapularis* (DS), *extensor carpi radialis* (ECR), *extensor antebrachii et carpi ulnaris* (EACU), *extensor digitorum* (ED), *flexor antebrachii et carpi radialis* (FACR), *flexor antebrachii et carpi ulnaris* (FACU), *flexor digitorum communis* (FDC), *humeroantebrachialis* (HB), *latissimus dorsi* (LD), *pectoralis* (P), *procoracohumeralis* (PCH), *pronator quadratus* (PQ), *subcoracoscapularis* (SCS), *supracoracoideus* (SC), *triceps* (T), *triceps humeralis* (TH).

## V. RECONSTRUCTION OF PECTORAL APPENDICULAR MUSCLES IN THE LCA OF TETRAPODOMORPHA, TETRAPODA, AND CROWN TETRAPODS

According to the strictest criteria of EPB, a muscle is inferred to be present in a fossil taxon only if the homologous muscle and its osteological correlate are present in both bracket taxa, and the homologous osteological correlate is present in the fossil taxon ('Level I inference' *sensu* Witmer, 1995). In a 'Level II' inference, the soft tissue is found in the extant sister group but not in the outgroup. ('Level II' inferences, in which the soft tissue is found in the extant sister group but not associated with an osteological correlate, were coded as '?' in the fossil taxa.) We used parsimony-based character mapping, which uses the same principle of maximum parsimony but includes many more taxa (both fossil and extant) in addition to the bracket taxa in its calculations (Hutchinson, 2001). The proposed homologous correlates were coded as character states in a matrix including all taxa we surveyed (Tables S1–3). For example, the character states for the insertion of the *pectoralis* or its homologue(s) were: 'elbow' joint capsule (and possibly ventral process) (0); ventral process only (1); highest point on oblique ventral ridge (2); pectoralis process (3); deltopectoral crest, sometimes with distinct scar (4). We also included correlates identified either as specific muscle attachments or as homologous with correlates identified as specific muscle attachments by other studies. Next, the characters were optimized onto a phylogeny of the group using the software Mesquite (Maddison & Maddison, 2017). Both maximum parsimony and maximum likelihood methods were employed. Thus, these reconstructions are supported both by soft tissue homology between extant sarcopterygian fish and tetrapods and by the osteological features preserved in the fossil record. We did not reconstruct any muscles based

on 'Level III' inferences, in which a proposed soft tissue is not present in any of the extant bracketing taxa.

For the purpose of using EPB for fossil reconstruction, *Neoceratodus forsteri* and *Latimeria chalumnae* represent extant sarcopterygian fish, while the salamanders *Ambystoma mexicanum* and *Salamanca salamandra*, the lizard *Iguana iguana*, and the lepidosaurian reptile *Sphenodon punctatus* represent extant tetrapods (Table 1). We include both a terrestrial (*S. salamandra*) and an aquatic (*A. mexicanum*) salamander to represent extant lissamphibians because salamanders are hypothesized to display a more plesiomorphic limb musculoskeletal configuration among tetrapods (Miner, 1925; Diogo & Tanaka, 2014; Diogo *et al.*, 2015). Among amniotes, we include *Sphenodon* as a representative of Rhynchocephalia, the extant sister group of all other lepidosaurs (i.e. squamates, including lizards and snakes) and thus hypothesized to retain a more plesiomorphic limb muscular configuration among extant reptiles (Miner, 1925; Russell & Bauer, 2008; Diogo & Abdala, 2010). We also include *Iguana* because it is one of the best-studied squamates and represents a generalized muscular configuration among lizards (Russell & Bauer, 2008).

The phylogeny used for character mapping was based on Ruta, Jeffery & Coates (2003) and Ruta (2011) because their analysis was most complete in terms of taxon sampling. An alternative phylogeny based on Ahlberg *et al.* (2008) was also tested, but this affected the results only slightly, as described below.

Seven pectoral appendicular muscles were reconstructed in the LCA of Tetrapodomorpha: proximal, middle, and distal divisions of superficial fin adductors (red) and abductors (green) and deep adductor (purple) (Fig. 11A, B). Because homologous muscles or muscle groups are present in both extant lobe-finned fish and tetrapods, this reconstruction is equivalent to a Level I inference *sensu* Witmer (1995). Nine appendicular muscles attach to the pectoral girdle,



Table 4. Character mapping of osteological correlates on pectoral girdle. ‘Uncertain’ results indicate three or more possibilities and/or cases in which the muscle may or may not attach to the pectoral girdle. Abbreviations: insertion (i), origin (o), last common ancestor (LCA).

Character	LCA Sarcoptrygii	LCA Tetrapodomorpha	LCA Tetrapoda	LCA crown Tetrapoda
1 <i>Coracoradialis</i> (o)	ridge immediately ventral to articular process, or with supracoracoideus	ridge or facet immediately ventral to articular process, or anterior ventral coracoid		Anterior ventral coracoid
2 <i>Supracoracoideus</i> (o)	medial scapulocoracoid ventral to articular process		medial scapulocoracoid ventral to articular process, or anterior ventral coracoid	Anterior ventral coracoid
3 <i>Subcoracoscapularis</i> (o)	ridge or facet immediately dorsal to articular process		triangular region posterior to ridge extending dorsally from supraglenoid buttress	
4 <i>Procoracohumeralis</i> (o)	dorsal process of scapulocoracoid		fossa on dorsolateral scapulocoracoid	
5 <i>Coracobrachialis longus</i> (o)	Uncertain	ridge or thickening on cleithrum ventral to articular process	posteroventral continuation of coracoid plate	
6 <i>Coracobrachialis brevis</i> (o)			Uncertain	posterior/medial ventral coracoid
7 <i>Pectoralis</i> (o)	ventral to articular process: from ridge or thickening on medial cleithrum, or from medial face of clavicle, cleithrum, and scapulocoracoid	ridge or thickening on cleithrum ventral to articular process	ridge or thickening on medial cleithrum ventral to articular process, and/or rugose, recessed region on posterolateral wings of interclavicle	rugose, recessed region on posterolateral wings of interclavicle, and/or outer surface of sternum and clavicle
8 <i>Triceps scapularis</i> (o)	medial cleithrum and scapulocoracoid dorsal to articular process	medial cleithrum and scapulocoracoid dorsal to articular process, or lateral face of scapula adjacent to glenoid		lateral face of scapula adjacent to glenoid
9 <i>Triceps coracoideus</i> (o)	dorsal to articular process: from ridge or thickening on posterolateral border of cleithrum, or from medial cleithrum and scapulocoracoid		Uncertain	posterior tuberosity/angle of coracoid
10 <i>Deltoideus scapularis</i> (o)	ridge or thickening on posterolateral border of cleithrum dorsal to articular process			dorsolateral surface of scapula/suprascapula
11 <i>Latissimus dorsi</i> (o)	ridge or thickening on posterolateral border of cleithrum dorsal to articular process, or medial face of cleithrum and scapulocoracoid dorsal to articular process	ridge or thickening on posterolateral border of cleithrum dorsal to articular process	Uncertain	no origin from girdle

humerus, radius, and/or ulna in *Latimeria*, and four do so in *Neoceratodus* (Fig. 5A, B). Two of these muscles, the *adductor superficialis* and *abductor superficialis* (red and green, respectively, in Fig. 5A–D, including segmented muscles in *Neoceratodus*), are partially divided into proximal, middle, and distal portions with attachments onto the humerus and ulna (additional divisions attach more distally on the fin). All but two of the muscles and divisions present in both *Latimeria* and *Neoceratodus* are hypothesized to be homologous with muscles or muscle groups in tetrapods (Diogo *et al.*, 2016); the exceptions are the distal portions of the superficial adductors and abductors. We were able to trace homologous osteological correlates of origins and/or insertions to the LCA of extant sarcopterygians for proximal and middle

portions of the *adductor superficialis*, *abductor superficialis*, *adductor profundus*, and *abductor profundus* (red, green, purple, and blue, respectively, in Fig. 11A, B). Only the proximal and middle portions of the *adductor superficialis* left traceable osteological correlates for both origin and insertion. *Pronator 1* could be reconstructed only provisionally because it is present in *Latimeria* but not in *Neoceratodus*. The remaining homologous muscles that attach to the humerus, radius, and/or ulna (*pterygialis cranialis*, *pterygialis caudalis*, *supinator 1*, *supinator 2*, and *pronator 2*) may have changed too much to be traced, their homologies may be mistaken, or they simply may not consistently leave osteological correlates.

Twelve additional muscles were reconstructed in the LCA of Tetrapoda (Tables 4–6, Fig. 11C, D). Because these



Table 5. Character mapping of osteological correlates on humerus. ‘Uncertain’ results indicate three or more possibilities and/or cases in which the muscle may or may not attach to the humerus. Abbreviations: insertion (i), origin (o), last common ancestor (LCA).

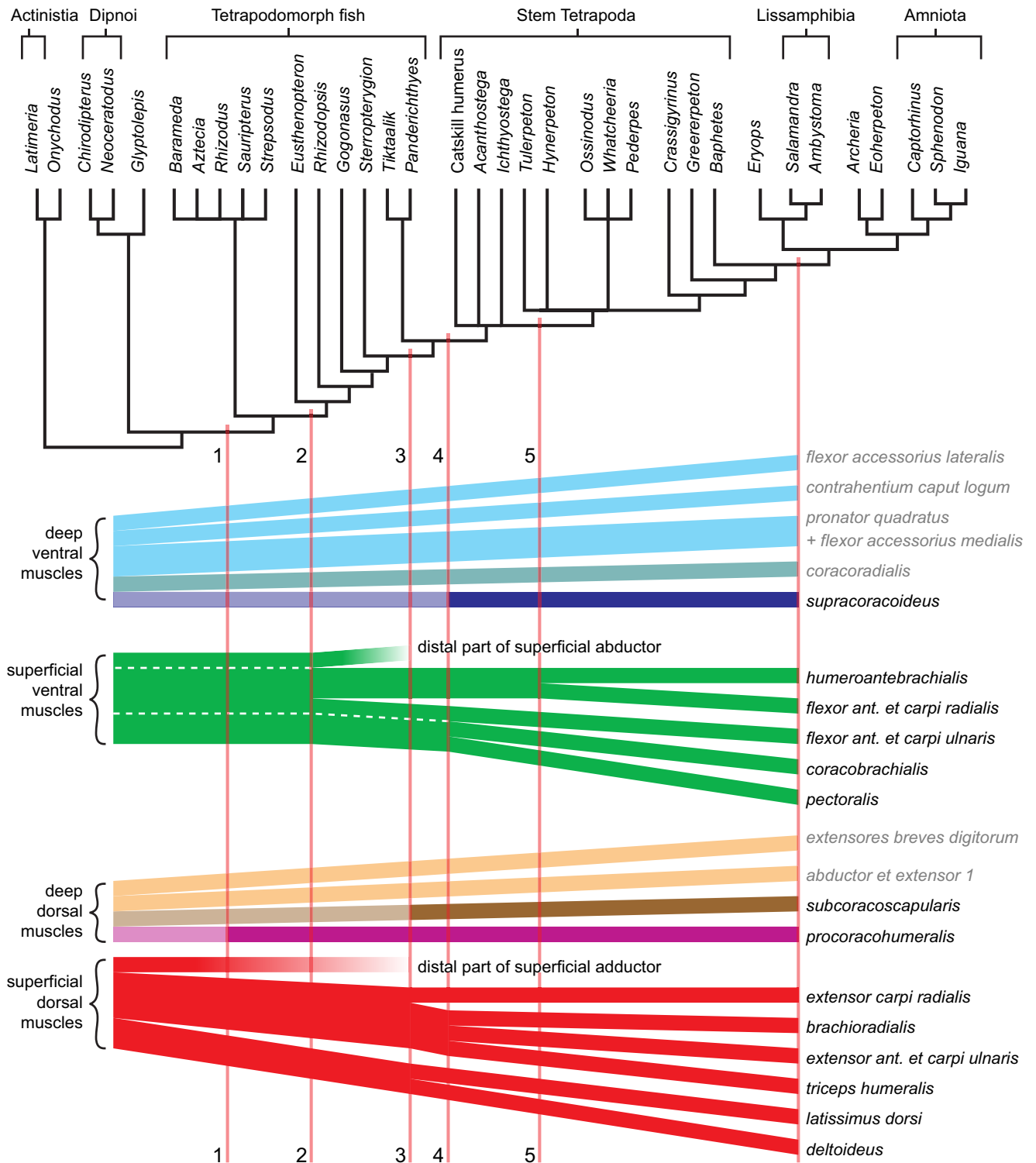
Character	LCA Sarcopterygii	LCA Tetrapodomorpha	LCA Tetrapoda	LCA crown Tetrapoda
1 <i>Pectoralis</i> (i)	ventral process	highest point on oblique ventral ridge	pectoralis process	deltopectoral crest
2 <i>Coracobrachialis</i> (i)		ventral process, or shallow recess and/or scarring on posterior proximal ventral surface	shallow recess and/or scarring on posterior proximal ventral surface	posterior/medial surface of distal humerus
3 <i>Flexor digitorum</i> (o)		oblique ventral ridge and/or entepicondyle	entepicondyle	
4 <i>Flexor carpi ulnaris</i> (o)		no attachment to humerus	oblique ventral ridge and/or entepicondyle	entepicondyle
5 <i>Flexor carpi radialis</i> (o)				deltopectoral crest or scars/tuberosity just distal to it
6 <i>Humeroantibrachialis</i> (o)				
7 <i>Supracoracoideus</i> (i)	Uncertain		shallow recess and/or the ridge that marks its posterior border on anterior proximal ventral surface	deltopectoral crest
8 <i>Coracoradialis</i> (i)			Uncertain	
9 <i>Flexor accessorius medialis</i> (o)			Uncertain	no attachment to humerus
10 <i>Latissimus dorsi</i> (i)			latissimus dorsi process	
11 <i>Deltoides scapularis</i> (i)	dorsal process or ridge		deltoid process or deltopectoral crest	deltopectoral crest
12 <i>Brachioradialis</i> (o)	Uncertain		supinator process or ridge	
13 <i>Extensor carpi radialis</i> (o)	Uncertain	ectepicondylar region	scar or facet on extensor surface distal to supinator ridge	ectepicondyle
14 <i>Extensor digitorum</i> (o)			ectepicondyle	ectepicondyle or anterior humeral shaft
15 <i>Triceps humeralis lateralis</i> (o)				dorsal humeral shaft
16 <i>Triceps humeralis medialis</i> (o)				
17 <i>Extensor carpi ulnaris</i> (o)	ectepicondylar region		ectepicondyle	
18 <i>Procoracohumeralis</i> (i)	Uncertain	scapulohumeral depression and/or rugose ridge posterior to it		
19 <i>Subcoracoscapularis</i> (i)		Uncertain	small process below humeral head on posterior edge, or concavity posterior to scapulohumeral depression	concavity posterior to scapulohumeral depression, or crista dorsalis
20 <i>Abductor et extensor D1</i> (o)		no attachment to humerus		

Table 6. Character mapping of osteological correlates on radius and ulna. ‘Uncertain’ results indicate three or more possibilities and/or cases in which the muscle may or may not attach to the radius or ulna. Abbreviations: insertion (i), origin (o).

Character		LCA Sarcopterygii	LCA Tetrapodomorpha	LCA Tetrapoda	LCA crown Tetrapoda
1	<i>Triceps coracoideus</i> (i)	dorsal process of ulna	Uncertain	olecranon process	
2	<i>Triceps scapularis</i> (i)				
3	<i>Triceps humeralis lateralis</i> (i)	Uncertain			
4	<i>Triceps humeralis medialis</i> (i)				
5	<i>Extensor carpi ulnaris</i> (i)			dorsal aspect of posterior ulnar flange/crest	dorsal aspect of posterior ulnar flange/crest or distal end of ulna
6	<i>Flexor carpi ulnaris</i> (i)	ventral process of ulna	ventral aspect of posterior ulnar flange/crest	ridge on flexor side of ulna	
7	<i>Coracoradialis</i> (i)	Uncertain			
8	<i>Flexor accessorius medialis</i> (o)	no attachment to radius or ulna	Uncertain		distal 1/2 of ventral ulna
9	<i>Flexor accessorius lateralis</i> (o)	Uncertain			
10	<i>Contraheptium caput longum</i> (o)	no attachment to radius or ulna			proximal ventral ulna
11	<i>Pronator quadratus</i> (o)	no attachment to ulna			mesial side of ulna
12	<i>Subcoracoscapularis</i> (i)	Uncertain	no attachment to radius or ulna		
13	<i>Abductor et extensor D1</i> (o)	no attachment to radius or ulna	Uncertain		distal end of ulna
14	<i>Extensores breves digitorum</i> (o)	no attachment to radius or ulna			
15	<i>Humeroantibrachialis</i> (i)	Uncertain	Uncertain	ventral process or ventral median ridge of radius	ventral median ridge of radius
16	<i>Flexor carpi radialis</i> (i)			between ventral radial crest and ventromesial ridge	flexor side of radius
17	<i>Brachioradialis</i> (i)	dorsal process of ulna	dorsal process of ulna, or between dorsomesial and proximoventral radial ridges	between dorsomesial and proximoventral radial ridges	lateral surface of radius
18	<i>Extensor carpi radialis</i> (i)				distal or entire surface of lateral radius
19	<i>Pronator quadratus</i> (i)	Uncertain			ridge on medial flexor side of radius, or distal 3/4 of lateral surface of radius
20	<i>Abductor et extensor D1</i> (i)	Uncertain	no attachment to radius or ulna		

muscles are present in extant tetrapods (ingroup) but not in extant lobe-finned fish (outgroup), this reconstruction is equivalent to a Level II inference *sensu* Witmer (1995). However, all 12 muscles are subdivisions of larger muscle masses present in extant lobe-finned fishes. For example, the distal portion of the superficial dorsal muscle mass which originates from the ectepicondyle is divided into the *triceps humeralis*, *triceps scapularis*, *extensor antebrachii et carpi ulnaris*, *extensor digitorum*, *extensor carpi radialis*, and *brachioradialis* (Fig. 11C, D) based on osteological correlates for insertion of these individual muscles present in stem tetrapods.

Based on the order in which their correlates appear in the phylogeny, we inferred an evolutionary sequence of differentiation of the pectoral appendicular muscles at specific nodes (Fig. 12). The reconstructed character state for node 1 (Tetrapodomorpha), as detailed in Tables 4–6, includes separate dorsal ridge and ectepicondylar regions but only a single ventral humeral ridge, indicating that the dorsal superficial shoulder and arm musculature was already separated but that the ventral superficial musculature may not have been. At node 2 (Eotetrapodiformes), the ventral process of the radius appeared, indicating separation of radial and ulnar/distal fin flexors. At node 3 (Elpistostegalia), the



**Fig. 12.** Hypothetical sequence of muscle differentiation from superficial and deep dorsal and ventral muscle masses based on the results of mapping osteological correlates onto the phylogeny of Ruta *et al.* (2003) and Ruta (2011). See text for specific osteological correlates. Colours correspond to Fig. 5. Dashed lines indicate partial separation of muscles by tendinous intersections. Muscles in grey text are inferred to be present based on homology but not associated with osteological correlates. Numbers 1–5 along the bottom of the figure indicate key nodes along the phylogeny discussed in the text.

latissimus dorsi process appeared, indicating the separation of the *latissimus dorsi* and *deltoideus*, a scar or facet appeared distal to the supinator ridge, indicating the separation of the *extensor carpi radialis* and *brachioradialis*, and the first individual osteological correlate of the *subcoracoscapularis*, a triangular region on the scapulocoracoid dorsal and posterior to the glenoid, appeared. At node 4 (Tetrapoda), a distinct pectoralis process and coracobrachialis fossa appeared on the humerus, indicating the separation of the *coracobrachialis* and *pectoralis*, and the olecranon process and posterior ulnar crest appeared, indicating the separation of the *triceps* and *extensor antebrachii et carpi ulnaris*. At node 5, the ventral median ridge of the radius appeared, indicating the separation of the *humeroantebrachialis* and *flexor antebrachii et carpi radialis*.

In most cases, the timing and sequence of these events was unaffected by the choice of phylogeny and reconstruction method. However, using Ahlberg *et al.*'s (2008) phylogeny (Tables S4–S6) (combined with the interpretation of the Catskill humerus presented in Ahlberg, 2011) delays the appearance of the latissimus dorsi process and the coracobrachialis fossa of the humerus to the node leading to *Ichthyostega* and more crownward tetrapods. These differences were probably caused mainly by the placement of the Catskill humerus: while Ruta (2011) placed it in a polytomy with *Acanthostega* and *Ichthyostega*, Ahlberg (2011) considered the Catskill humerus to be the earliest tetrapod humerus. Therefore, aspects of the Catskill humerus morphology are more likely to have been interpreted as ancestral for tetrapods according to the analysis using the second phylogeny. In the maximum likelihood analysis, using the alternative phylogeny delays the appearance of the osteological correlate of the origin of the *subcoracoscapularis* to the node leading to *Acanthostega* and more-crownward tetrapods.

Based on our review and analysis, the presence of individual muscles in particular groups can be assigned different levels of confidence. For example, in the tetrapodomorph fish *Eusthenopteron*, the muscles that can be reconstructed with the highest degree of confidence are those that correspond to muscles/muscle structures inferred to be present in the LCA of sarcopterygians according to Diogo *et al.* (2016) and for which osteological correlates have been identified in fossil remains of *Eusthenopteron*: the *deltoideus*, *pectoralis*, forearm flexors, and forearm extensors. The *procoracohumeralis* and *supracoracoideus* can be reconstructed based on the homology hypotheses of Diogo *et al.* (2016) because similar muscles are present in extant lungfish, coelacanth, and tetrapods. Radial and ulnar flexors and extensors can be restored with slightly less confidence because their osteological correlates appear in the tetrapod lineage before the node leading to *Eusthenopteron* based on character mapping (node 3 in Fig. 12) but were not present in earlier diverging tetrapodomorph fish. The *subcoracoscapularis*, *coracobrachialis longus and brevis*, *latissimus dorsi*, *triceps*, and other individual forearm muscles were reconstructed by Andrews & Westoll (1970a), but we did not find compelling evidence that they existed as separate muscles in early tetrapodomorph fish. In the stem tetrapod *Ossinodus*,

the same six muscles/muscle masses (*deltoideus*, *pectoralis*, forearm flexors, forearm extensors, *procoracohumeralis*, and *supracoracoideus*) can be reconstructed with the highest degree of confidence because their correlates are present in this taxon as well (Bishop, 2014). Combining the results of character mapping (Fig. 12) with the scars present in *Ossinodus*, we can fairly confidently reconstruct the *latissimus dorsi*, *subcoracoscapularis*, *triceps*, *coracobrachialis*, *humeroantebrachialis*, *brachioradialis*, *extensor carpi radialis*, *extensor antebrachii et carpi ulnaris*, and *flexor antebrachii et carpi radialis*. Indeed, all of the appendicular muscles reconstructed by Bishop (2014) were supported by the results of our analysis.

## VI. CONCLUSIONS

(1) The results of our analysis are largely congruent with previous palaeontological and comparative work, but they add an additional layer of detail. Combined with the results of Diogo *et al.* (2016), they support the hypothesis of Ahlberg (1989) that the dorsal and ventral processes of the humerus are a synapomorphy of sarcopterygians and that they are homologous with the entepicondyle and ectepicondyle of tetrapods. Specifically, in early tetrapodomorphs (e.g. rhizodontids), the dorsal process gave rise to the ectepicondyle and deltoid/supinator ridge and the ventral process to the oblique ventral ridge and entepicondyle, mirroring the complete division of the superficial muscles into proximal and distal portions. In later tetrapodomorph fish and stem tetrapods, as described previously (Shubin *et al.*, 2004; Boisvert, 2009), the deltoid process and supinator process became separate, the latissimus dorsi process and scapulohumeral depression emerged, and the pectoralis process became distinct from the oblique ventral ridge, mirroring the initial breakup of the proximal superficial muscle masses.

(2) Reciprocally, the fossil information allows us to add to the homology hypotheses of Diogo *et al.* (2016). That study postulated that the superficial adductors and abductors of lobe-finned fish gave rise to both proximal and distal superficial limb muscles, and we can now add that the first two segments of these muscles, divided by tendinous intersections, are probably homologous to the superficial shoulder and forearm musculature, respectively (Fig. 12). The distal segments were either lost over the fins-to-limbs transition with the loss of the lepidotrichia, or they were incorporated into the intrinsic autopodial musculature (Diogo *et al.*, 2016).

(3) While the fossil record is congruent with the persistence of the superficial and deep muscle layers throughout sarcopterygian history, as postulated by Diogo *et al.* (2016), we did not find compelling fossil evidence to support the persistence of pre- and postaxial muscles or pronators/supinators in the tetrapod lineage. For example, in the tetrapodomorph fish that we surveyed, no scars were described on the preaxial or postaxial humerus, other than the entepicondyle. Likewise, we did not find fossil evidence that *pronator 1* and *supinator 1* (hypothesized to be homologous



with the *subcoracoscapularis* and *coracoradialis*, respectively) persisted in the tetrapod lineage. However, it is very possible that homologues of these two muscles were present in the LCA of extant sarcopterygians and were subsequently lost in the tetrapod lineage.

(4) Our review of the evidence suggests that reconstructions that show tetrapod-like pectoral appendicular muscles in tetrapodomorph fish – such as *Eusthenopteron* – should be regarded as highly speculative, whereas reconstructions of tetrapod-like pectoral limb muscles in stem tetrapods – such as *Ossinodus* – are supported by both fossil and comparative data.

## VII. ACKNOWLEDGEMENTS

We thank museums and staff for access to fossil material: The Universität Tübingen, Macquarie University, The Natural History Museum, London, Academy of Natural Sciences of Philadelphia, Geological Museum in Copenhagen, Museum of Comparative Zoology, Cambridge, and University of Glasgow Hunterian Museum. J.L.M. thanks the American Association of Anatomists (US) for funding aspects of this research under the AAA Postdoctoral Fellowship and Short-term Visiting Scholarship. J.R.H. and S.E.P. thank the Natural Environment Research Council (UK) for funding aspects of this research under grant number NE/K004751/1.

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## IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Fig. S1.** Potential osteological correlates on the left pectoral girdle of *Pederpes finneyae*, the right pectoral girdle of *Acanthostega gunnari*, the left pectoral girdle of *Tiktaalik roseae*,

the left ulna of *Acanthostega gunnari*, and the right pectoral girdle of *Eryops*.

**Table S1.** Character matrix for pectoral girdle.

**Table S2.** Character matrix for humerus.

**Table S3.** Character matrix for radius/ulna.

**Table S4.** Character mapping of osteological correlates on pectoral girdle using alternative phylogeny.

**Table S5.** Character mapping of osteological correlates on humerus using alternative phylogeny.

**Table S6.** Character mapping of osteological correlates on radius and ulna using alternative phylogeny.

(Received 14 January 2017; revised 2 October 2017; accepted 13 October 2017)