Stem sarcopterygians have primitive polybasal fin articulation

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Among osteichthyan fishes e.g. paddlefish and bowfins have paired fins with three endoskeletal components (pro-, meso- and metapterygia) articulating with polybasal shoulder girdles, while sarcopterygian fishes (lungfish, coelacanths and relatives) have paired fins with one endoskeletal component (metapterygium) articulating with monobasal shoulder girdles. In the fin-limb transition, the origin of the sarcopterygian paired fins triggered new possibilities of fin articulation and movement, and established the proximal segments (stylopod and zeugopod) of the presumptive tetrapod limb. Several authors have stated that the monobasal paired fins in sarcopterygians evolved from a primitive polybasal condition. However, the fossil record has been silent on whether and when the inferred transition took place. Here we describe three-dimensionally preserved shoulder girdles of two stem sarcopterygians (Psarolepis and Achooania) from the Lower Devonian of Yunnan, which demonstrate that stem sarcopterygians have polybasal pectoral fin articulation as in basal actinopterygians. This finding provides a phylogenetic and temporal constraint for studying the origin of the stylopod, which must have originated within the stem sarcopterygian lineage through the loss of the propterygium and mesopterygium.

Keywords: sarcopterygians; fin-limb transition; stylopod; shoulder girdle; polybasal fin articulation

1. INTRODUCTION

Crown sarcopterygians include all living lungfish, coelacanths and tetrapods and all the extinct descendants of their last common ancestor. Stem sarcopterygians are fossil forms phylogenetically basal to crown sarcopterygians and often provide clues to the origin of evolutionary novelties in crown sarcopterygians. Whether stem sarcopterygians have monobasal or polybasal paired fins is critical for studying the origin of the stylopod, the proximal segment of the metapterygial endoskeleton in the paired fins of sarcopterygian fishes and in tetrapod limbs. Speculations on the origin of the sarcopterygian fin...
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actinopterygians and consistent with the position of *Psarolepis* as a stem sarcopterygian.

(b) Shoulder girdle of *Achoania*
Specimen V15545 (figure 1h–k) resembles the shoulder girdle of *Psarolepis* in general, but differs in the shorter length of the pectoral spine, as well as in the larger size and more robust shape of the cleithrum. These differences in size and stoutness resemble those observed between *Psarolepis* and *Achoania* in cranial and mandibular materials (Yu 1998; Zhu et al. 1999, 2001; Zhu & Yu 2004). The pore size on the cosmine surface resembles more closely that of *Achoania* than that of *Psarolepis* and other large-pored sarcopterygians (Stylechthys and Meemanni; Zhu et al. 2006). Based on these features, V15545 is tentatively referred to *Achoania*. As in *Psarolepis*, the scapulocoracoid is a massive plate pierced internally by two rows of openings (c.dm and c.vm; figure 1h). The articular crest bears three facets, instead of four as in *Psarolepis*. The facets for the metapterygium and the propterygium (met and pro; figure 1j,k) resemble those in *Psarolepis*. However, only one facet (mes; figure 1j,k) for the mesopterygium or mesopterygial radial(s) can be identified.

4. DISCUSSION
The discovery of the polybasal shoulder girdle in stem sarcopterygians has wide implications for studying the evolution of sarcopterygians in general and the fin–limb transition in particular.

The finding demonstrates that stem sarcopterygians have polybasal pectoral fin articulation as in chondrichthyans and basal actinopterygians such as *Mimia*, paddlefish and bowfins (figure 2). Consequently, the origin of the monobasal sarcopterygian fin must have occurred at a point crowndward to *Psarolepis* and *Achoania*, instead of that at the split between sarcopterygians and actinopterygians. The notion that the monobasal, lobed fin characterizes all sarcopterygians (Romer 1955; Rosen et al. 1981; Janvier 1996) should be revised.

The polybasal fin articulation in stem sarcopterygians adds more primitive features to the sarcopterygian morphotype (Zhu et al. 2001, 2006), and lends support to the hypothesis that the presence of three pterygial radials represents the primitive condition for osteichthyans (Janvier 1996), with subsequent loss of the metapterygium in advanced actinopterygians (teleosts; Ma bee 2000) and loss of the propterygium and mesopterygium in crown sarcopterygians (including tetrapods).

Loss of the propterygium and mesopterygium signifies the origin of the stylopod, and is developmentally achieved through the loss of the endoskeletal disc, a chondrogenic plate of mesenchymal cells (Davis et al. 2004). The phylogenetic constraint provided by stem sarcopterygians will help the study of the stylopod origin to catch up with the study of the autopod origin (Wagner & Chiu 2001; Shubin et al. 2006; Davis et al. 2007; Johanson et al. 2007) by focusing more on phylogenetically appropriate forms in fossil and developmental studies.

Figure 1. Polybasal shoulder girdles of (a–g) *Psarolepis* and (h–k) *Achoania* with articular facets for multiple pterygial components. (a–c) Right cleithrum with scapulocoracoid (*Psarolepis*, IVPP V15544.1) in (a) lateral, (b) medial and (c) posterior views. (d,e) Right cleithrum with scapulocoracoid (*Psarolepis*, V15544.2) in (d) lateral and (e) posteriormedial views. (f,g) Illustrative drawings of V15544.2 to emphasize structures in (f) posteriormedial and (g) medial views. (h–j) Left cleithrum with scapulocoracoid (*Achoania*, V15545) in (h) medial, (i) lateral and (j) posterior views. (k) Illustrative drawing of V15545 in posterior view. c.dm, dorsomedial canals for pterygial nerves and vessels; c.vm, ventromedial canals for pterygial nerves and vessels; cr.art, articular crest of scapulocoracoid; d.perc, pericardial depression; f.md, dorsal muscle fossa; f.mv, ventral muscle fossa; mes, articular facet for mesopterygium or mesopterygial radial(s); met, articular facet for metapterygium; pbl, postbranchial lamina of cleithrum; pro, articular facet for propterygium; ps, pectoral spine of cleithrum; sc, scapulocoracoid; vl, ventral lamina of cleithrum.

For instance, a fibroblast growth factor gene (fgf24) involved in fin outgrowth is present in zebrafish and possibly shark but absent in mouse, chick and human (Draper et al. 2003; Fischer et al. 2003; Mercader 2007). With the presence of fgf24 presumed to be a primitive gnathostome condition, subsequently lost after sarcopterygians diverged from actinopterygians (Draper et al. 2003), it is tempting to suggest that the loss of pr+ and mesopterygia may have been correlated with the loss of fgf24 (figure 2), a molecular event that might have occurred crownward to Psarolepis and Achoania, with a minimum age of 416 Myr ago as established by the earliest record of crown sarcopterygians (Zhu & Fan 1995). The distribution pattern of fgf24 in paddlefish, bichirs, lungfish and coelacanths will provide a potential test of this suggestion.

Figure 2. Composite cladogram showing pectoral fin–limb and girdle conditions among gnathostome groups. The monobasal lobe fins or stylopod originated in the internode between stem sarcopterygians (Psarolepis and Achoania) and crown sarcopterygians, with a minimum age of 416 Myr ago. Crown sarcopterygians (purple) lack pro- and mesopterygia. Lineages in blue possess pro- and mesopterygia. Red line indicates the metapterygial axis, green shading the metapterygium and grey shading the scapulocoracoid. Minus sign indicates loss of pterygial components. Inset shows the polybasal shoulder girdle of Mimia in posterior view (Gardiner 1984). Top bars summarize the distribution of the endoskeletal disc (first row) and of the fgf24 gene (second row): blue for the presence; purple for the absence; light blue or purple for the inferred presence or absence; and asterisk for the probable presence of fgf24 orthologue in shark (Draper et al. 2003). The likely presence of the endoskeletal disc in osteostracans is based on Janvier et al. (2004), suggesting that stem gnathostomes and crown sarcopterygians may have different developmental patterns for pectoral fins. Drawings adapted and redrawn from Jarvik (1980), Gardiner (1984), Janvier (1996), Mabee (2000), Clack (2002), Shubin et al. (2006) and Friedman et al. (2007).

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