The myth of dorsal ribs in gnathostome vertebrates

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Traditionally, two types of rib are distinguished in gnathostomes: dorsal (upper) and ventral (lower, pleural) ribs. They are defined according to their position in the connective tissue system of the body: dorsal ribs develop at the intersection of the serially arranged myosepta with the horizontal septum that separates epaxial from hypaxial musculature, whereas ventral ribs develop at the intersection of myosepta with the peritoneum and usually encircle the body cavity. Distribution of rib types among gnathostomes has traditionally been reported as follows: elasmobranchs have dorsal ribs; all Actinopterygii have only ventral ribs with the exception of polypterids, and two subgroups of teleosts, which supposedly also have dorsal ribs; within Sarcopterygii tetrapods have dorsal ribs, whereas dipnoans have ventral ribs. Here, we report the development of ribs in polypterids, a taxon playing a crucial role in discussions on rib homology. We demonstrate that putative dorsal ribs of polypterids have a unique ontogeny and represent an autapomorphy of this taxon. We discuss previous hypotheses of rib homology and offer a more plausible (i.e. more parsimonious) alternative to the conventional interpretation. We conclude that dorsal ribs do not exist and that ribs of gnathostomes are ventral ribs.

Keywords: dorsal ribs; ventral ribs; polypterids; gnathostomes

1. INTRODUCTION

Ribs are elongate, serially arranged endoskeletal elements located in the connective tissue system of gnathostome vertebrates. They are usually preformed in cartilage, ossify later in development and articulate proximally with the vertebral column. Ribs are considered to be of two kinds: (i) upper or dorsal and (ii) lower, ventral or pleural.

In all major textbooks on vertebrate morphology (e.g. Goodrich 1930; Romer & Parsons 1978; Liem *et al.* 2000), the two sets of gnathostome ribs are distinguished in the following way: dorsal ribs ossify and are situated at the intersection of the serially arranged myosepta with the horizontal septum that separates the epaxial from the hypaxial musculature. Ventral ribs ossify and are situated at the intersection of the myosepta with the peritoneum

so that they usually encircle the body cavity. This topographic criterion of rib distinction originated with the publications of the German anatomists Goette (1878) and Göppert (1895), and was adopted by many subsequent researchers. Solely Emelianov (1935, 1936) pointed out another criterion to distinguish the two sets of ribs, i.e. the direction of ontogenetic growth: dorsal ribs originate in the periphery and grow towards the axial skeleton, whereas ventral ribs originate close to the axial skeleton and grow towards the periphery.

Although reaching different results (see § 4; figure 2a,b), both these hypotheses of rib homology share the idea that there are two sets of ribs among vertebrates. In the discussion about rib homology, the polypterids or bichirs—the basalmost living actinopterygians (Gardiner & Schaeffer 1989)—have always played a pivotal role because they are exceptional among gnathostomes in possessing two sets of ribs (Goette 1878; Göppert 1895; Emelianov 1935; Rosen *et al.* 1981).

Extensive ontogenetic series of *Polypterus* and *Erpetoichthys* reared in captivity enabled us to study for the first time, to our knowledge, the development of the two series of ribs of these crucial taxa and to review and evaluate the different concepts of rib homology among vertebrates.

2. MATERIAL AND METHODS

All specimens were cleared and double stained (c&s) according to the protocol of Taylor & Van Dyke (1985). *Erpetoichthys calabaricus*: 26 specimens from 10 mm total length (TL) to 53 mm standard length (SL); *Polypterus ornatipinnis*: 67 specimens ranging from 10 mm TL to 63 mm SL; *Gymnarchus niloticus* 64 mm SL; *Anchoa mitchelli* 57.5 mm SL; and *Mallotus villosus* AMNH 26286, 135 mm SL. All specimens were photographed with a Zeiss Tessovar photomicroscope.

3. RESULTS

In representatives of the two Recent genera, *Polypterus* and *Erpetoichthys*, the putative dorsal ribs appear at ca. 15–17 mm SL in our c&s specimens. They arise as small nodules of cartilage situated at the periphery of the intersection between the myosepta and horizontal septum (figure 1a). The sequence of chondrification along the body axis is in a rostrocaudal direction. During subsequent development the nodules elongate slightly and start to ossify proximally. Ossification then extends into the tendinous structures that link the cartilages to the vertebral column so that most of the length of the dorsal rib is completed through membrane bone (figure 1b,c). Articulation of putative dorsal ribs is with the parapophyses of the vertebral column (figure 1b) that develop from separate ventral cartilages (basiventrals). At ca. 30 mm SL, the first scales, i.e. those of the lateral line, start to ossify in the skin around the distal cartilaginous end of the putative dorsal ribs. This connection is elaborated into a complex articulation in the adult fish.

Ventral ribs appear at around the same developmental stage (i.e. 15 mm) in *Polypterus* (figure 1c). They arise as elongate cartilages very closely attached to the lower face of the chorda. They also chondrify in a rostrocaudal sequence along the body. During subsequent development they elongate and grow towards the periphery.

In summary, ventral ribs of polypterids develop and are located as ribs in most other gnathostomes but their putative dorsal ribs are unique in having a cartilaginous distal end and most of the rib body ossifying in membrane bone.

Figure 1. Development and position of ribs, epicentral bones or cartilages, and chevrons in the anterior abdominal region of c&s specimens of selected actinopterygian taxa (blue, cartilage; red, bone). Scale bars, 0.5 mm. Abbreviations: chev, cartilaginous chevrons; epic, cartilaginous or bony epicentrals; lr, lower (ventral) ribs; 'ur', putative upper (dorsal) ribs. (a) *Erpetoichthys calabaricus* larva 16.0 mm SL, dorsal view. (b) *Erpetoichthys calabaricus* juvenile 42.0 mm SL, dorsal view. (c) *Polypterus ornatipinnis* larva 21 mm SL, ventro-lateral view. Note the distal cartilages of putative dorsal ribs and the proximal cartilages of ventral ribs. (d) *Mallotus villosus* 138 mm SL, lateral view. Note the epicentral cartilages in the horizontal septum. (e) *Anchoa mitchelli* 57.5 mm SL, lateral view. Note the cartilaginous chevrons at the distal end of the epicentral bones. (f) *Gymnarchus niloticus* juvenile 64 mm SL, lateral view. Note the shift in position of the ribs along the body.

4. DISCUSSION

The current hypothesis of distribution of rib types among gnathostome groups originated at the end of the nineteenth century (Goette 1878; Göppert 1895) when idealistic views in anatomy still prevailed. This was long before strict phylogenetic logic entered discussions about homology and evolution and before the importance of considering two criteria, structural similarity and phylogenetic congruence (Patterson 1982), for establishing homology was recognized. Goodrich's (1930) schematic representation of rib arrangement in an ideal gnathostome, based on Goette's (1878) and Göppert's (1895) hypothesis, has thus survived almost 100 years and has

entered modern textbooks on vertebrate morphology (e.g. Romer & Parsons 1978; Liem *et al.* 2000) virtually unchanged, although the phylogenetic incongruence of this hypothesis was noted previously (Schmalhausen 1968; Rosen *et al.* 1981; Gardiner 1984). Goette's (1878) and Göppert's (1895) hypothesis claims that elasmobranchs have dorsal ribs, *Polypterus* has both sorts of rib, most other actinopterygians have ventral ribs, but some teleosts are said to have dorsal ribs in addition, dipnoans have ventral ribs, and tetrapods have dorsal ribs.

A prerequisite for this current hypothesis is that dorsal and ventral ribs were present in the last common ancestor of all gnathostomes. The occurrence of two sets of ribs in

Figure 2. Three hypotheses of rib homologies plotted on a current phylogeny of gnathostomes (Janvier 1996). (a) Goette's and Göppert's hypothesis; (b) Emelianov's hypothesis; and (c) our hypothesis that stresses the singular origin of one rib type. Note that long ossified ventral ribs were only reported in some fossil Actinistia. Solid blue rectangle, upper ribs; solid red rectangle, lower ribs; blue outlined rectangle, reductions of upper ribs; red outlined rectangle, reduction of lower ribs; solid green rectangle, 'epicentrals'; solid black rectangle, epicentrals.

polypterids was usually cited in support of this idea (Göppert 1895; Goodrich 1930; Romer & Parsons 1978). However, if character distribution resulting from this hypothesis is mapped on the phylogenetic tree of gnathostomes, it yields an unlikely and unparsimonious scenario for rib evolution (figure 2a). Dorsal ribs must have been lost independently during evolution among actinopterygians in chondrosteans (sturgeons and paddlefish), ginglymodans (gars), halecomorphs (bowfin), and at least four

times in teleosts (advanced bony fishes). Dorsal ribs would also have to have been lost independently in dipnoans. Likewise, in chondrichthyans and several times in the tetrapod lineage ventral ribs must have been lost independently, so that losses of ribs add up to a total of 10 independent events.

The second, though less popular, scenario of rib homology by Emelianov (1935, 1936) accepts that there are two sets of ribs in vertebrates, but that direction of ontogenetic growth and not position is the criterion to distinguish them: dorsal ribs originate at the periphery and grow towards the axial skeleton, and ventral ribs originate close to the axial skeleton and grow towards the periphery. Following this ontogenetic criterion elasmobranchs have ventral ribs, actinopterygians have ventral ribs but only polypterids and teleosts have two sets of ribs, dipnoans have ventral ribs, urodeles have dorsal ribs, and caecilians and all amniotes have ventral ribs. As with the above hypothesis, Emelianov (1935) assumed that both sorts of rib must have been present in the last common ancestor of all gnathostomes. Mapping this distribution of rib types on a phylogenetic tree again yields an unparsimonious result (figure 2b). Dorsal ribs must have been lost independently in chondrichthyans, at least seven times in the different actinopterygian lineages, in dipnoans, in caecilians and in amniotes. Ventral ribs were lost in urodeles, so that this scenario requires 11 independent losses of ribs.

Our scenario of rib homology and evolution rests on the assumption that the last common ancestor of gnathostomes had one set of ribs, ventral ribs, that were located in the peritoneum and encircled the body cavity. The occurrence of long ossified ventral ribs among Actinistia is based on fossil taxa only; the extant *Latimeria* lacks ribs (Forey 1997). Other than in polypterids, putative dorsal ribs have been recorded previously from clupeomorph and protacanthopterygian teleosts (Göppert 1895; Emelianov 1935). In clupeomorphs they represent cartilaginous chevrons of irregular shape at the distal tip of epicentral intermuscular bones in the horizontal septum (figure 1e). Various protacanthopterygians have rod-like cartilaginous epicentrals in the horizontal septum (figure 1d). The presence of putative dorsal ribs of clupeomorphs and protacanthopterygians has been recently demonstrated to be autapomorphic features of the respective taxa (Patterson & Johnson 1995), due to their lack of structural similarity and their restricted phylogenetic occurrence in these two distantly related teleost subgroups.

Likewise, the putative dorsal ribs of polypterids are structurally and developmentally different from other gnathostome ribs and thus fail the initial test of similarity. They also fail the second test of homology, character congruence (Patterson 1982), as too many independent losses of ribs are required to explain the given character distribution in both scenarios. Our scenario needs only the two following assumptions: ventral ribs of living chondrichthyans have moved from their original peritoneal position to a more dorsal one, and ventral ribs of living lissamphibia have also moved into a more dorsal position. Both assumptions gain support from fossil evidence. Hybodontid and xenacanthid sharks, stem group elasmobranchs, had long ribs that most probably encircled the body cavity and therefore were previously interpreted as

ventral ribs (Maisey 1982). Although it is still unclear if the last common ancestor of tetrapods had short or long ribs (Coates 1996), at least the long ribs in *Ichthyostega* (Jarvik 1996), a stem group tetrapod, and in many stem group amphibians such as *Mastodonsaurus* (Schoch 1999) were most probably in a peritoneal position. Thus the dorsal position of the short ribs of living chondrichthyans and lissamphibia is probably secondary. The fact that long ventral ribs may shorten and shift into a more dorsal position is exemplified by the actinopterygian *Lepisosteus* (Emelianov 1935) and the teleost *Gymnarchus* (figure 1f). In both taxa posterior abdominal ribs are long and in a peritoneal position, but become shorter and shift to a more dorsal position anteriorly so that the distal ends of the first ribs are located deep in the musculature.

On the basis of all evidence at hand, our hypothesis of rib homology and evolution among gnathostomes is more parsimonious than the two hypotheses discussed above. We therefore conclude that all gnathostome ribs are homologous and that they represent only the ventral series.

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