

Development and growth in xenacanth sharks: new data from Upper Carboniferous of Bohemia

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Abstract

Articulated, nearly complete xenacanthids from the Westphalian D of Bohemia (Czech Republic) representing pre-adult and adult stages provide new information about the early development of xenacanths. Most of the specimens are juveniles of *Orthacanthus bohemicus* and adults of *Xenacanthus parallelus*. Study of the new material and comparison with other specimens previously described lead to a revision of several characters related to the dorsal spine and unpaired fins that are often used in phylogenetic analyses.

The new material indicates that the dorsal spine of members of Xenacanthidae, hitherto regarded as the cranial (occipital) spine, was initially formed in front of the dorsal fin, behind the pectoral girdle, in a fashion similar to the spine of the more primitive xenacanths Lebachacanthidae and Diplodoselachidae. The subsequent occipital location of the spine in sub-adult and adult of Xenacanthidae was achieved through differential growth of the proximal part of the spine early in ontogeny. In contrast, the dorsal spine of Diplodoselachidae and Lebachacanthidae is always located behind the pectoral girdle.

The new results support the presence of two dorsal and anal fins (anterior and posterior) as a synapomorphy of the clade formed by Lebachacanthidae and Xenacanthidae. The long anterior dorsal fin has traditionally been considered the only dorsal fin in xenacanths. This is the state in Diplodoselachidae only. The posterior dorsal fin has been considered the dorsal lobe of a diphycercal caudal fin or the dorsal part of the superior lobe of the heterocercal caudal fin. On the other hand, the posterior anal fin described here has previously been identified as the inferior lobe of a heterocercal caudal fin. There is no true caudal fin in Lebachacanthidae and Xenacanthidae, in contrast to the primitive Diplodoselachidae where a heterocercal caudal fin is well defined. The development of the posterior dorsal and anal fins is a novelty for Lebachacanthidae and Xenacanthidae and correlates with the caudal elongation of the straight vertebral column. A careful analysis of ontogenetic changes in the postcranial skeleton is needed to more clearly establish character states relating to the position and structure of anatomical elements.

Introduction

Bohemian material has been very important in the study of xenacanths, a group of elasmobranchs ranging from Early Carboniferous to Late Triassic. Xenacanth sharks were described for first time from isolated teeth (*Diplodus gibbosus*) and spines (*Pleuracanthus laevissimus* and *Orthacanthus cylindricus*) found in the Upper Carboniferous of the British Isles (BINNEY 1840, AGASSIZ 1833-1843). The fragmentary condition of the material led to erroneous ideas about this group of fishes. AGASSIZ mistook isolated denticulated spines of *Orthacanthus* and *Pleuracanthus* for the tail spines of rays. Fortunately, shortly after the first descriptions GOLDFUSS (1847) and BEYRICH (1848) studied a nearly complete xenacanth from a Lower Permian sandstone at Ruprechtice (=Ruppersdorf), in the Intra-Sudeten basin, Czech Republic. The specimen, assigned to the genus *Xenacanthus* (*X. decheni*) by BEYRICH (1848), showed a denticulated spine close to the occipital area of the neurocranium and for the first time provided correct information about the general morphology of xenacanths, a fossil group very distinct from others then known. Abundant material from Bohemia, in many cases representing articulated individuals, gave FRITSCH (1889, 1890) an opportunity to define the genera *Orthacanthus*, *Xenacanthus* and *Pleuracanthus* on the basis of spines, teeth, pharyngeal denticles and pectoral fins.

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