

PECTORAL FIN OF THE PALEOZOIC SHARK, *CLADOSELACHE*: NEW RECONSTRUCTION BASED ON A NEAR-COMPLETE SPECIMEN

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One of the most important inventions in vertebrate evolution is paired fins. Recent findings from studies of developmental genetics have shown that some, but not all, of the developmental mechanisms of tetrapod limbs are shared with those of elasmobranchs (e.g., Tanaka et al., 2002; Dahn et al., 2007; Freitas et al., 2007). This finding has focused renewed attention on fossil fins and limbs, especially in studies since ca. 2000 (e.g., Coates, 2003; Carr et al., 2010). *Cladoselache* is probably the most widely known Paleozoic shark-like Chondrichthyes; however, its anatomy is not known in the detail now available for taxa such as *Doliodus* (Miller et al., 2003; Maisey et al., 2009, 2014). In one of the earliest reports concerning the origin of paired fins, Woodward (1892) assumed that the pectoral fin of *Cladoselache* represents one of the least modified conditions of fish pectoral fins. Since that time, the pectoral fin structure of *Cladoselache* has been cited in many zoology, ichthyology, and paleontology textbooks as an example of a primitive form of chondrichthyan fin (e.g., Benton, 2004; Prothero, 2004; Moyle and Cech, 2012). However, our knowledge of the pectoral of *Cladoselache* fins has been based on reconstructions derived from specimens in which the exact morphology and arrangement of skeletal components in proximal portions of the fin are not well known.

The first reconstruction of the pectoral fin structure of *Cladoselache* was given by Dean (1894; Fig. 1A), wherein he described it as a broad-based triangular flap. Notably, he identified the presence of a basal cartilage, which is an endoskeletal fin support in extant sharks. He illustrated the basal cartilage as a segmented triangular cartilaginous plate, although its structural detail remained uncertain.

Bendix-Almgreen (1975) reexamined the *Cladoselache* specimens and provided a revised reconstruction of its pectoral fin (Fig. 1B) that differed significantly from Dean's (1894) description. He showed that six or more anterior radials were directly attached to the pectoral girdle and the posterior radials were supported by a single basal cartilage (metapterygium). He also proposed the presence of 'metapterygial axials,' arising from the posterior end of the basal cartilage. Recent phylogenetic and comparative studies have used this reconstruction (Coates and Sequeira, 2001a, 2001b; Maisey, 2008).

A specimen of *Cladoselache* held in the collection of the Cleveland Museum of Natural History (CMNH; Cleveland, Ohio, U.S.A.) has a complete pectoral fin with unambiguous morphology that differs from previous reconstructions. A full examination of this specimen, including complete basal cartilages, has enabled significant revision of the structure of the proximal endoskeleton of the *Cladoselache* fin.

MATERIALS AND METHODS

The specimen described in this study is designated CMNH 8114. Williams (1990) reported the gastric contents (three actinopterygians; *Kentuckia halavini*) of this specimen, but no detailed description of its skeletal anatomy has been provided thus far. The specimen is two-dimensionally preserved in black shale, and the skeletal elements are divided between the part and counterpart of the slab. It was collected from the 'Cleveland Shale' (Late Devonian) in 1966. The location of this specimen is at I-71 and W. 130th Street in Cleveland, Ohio. The preparation of this specimen was conducted by staff of the CMNH, using acid, mounted needles, and air scribes.

TAXONOMIC IDENTIFICATION

CMNH 8114 was identified as *Cladoselache* sp. based mainly on tooth morphology (Fig. 2A). The teeth of *Cladoselache* have the following features: (1) large, triangular, and slightly sigmoid median cusp, with a smooth and flat labial surface; (2) one or two pairs of lateral cusps that are much smaller than the median cusp; and (3) triangular projections on each side of the basioblabial depression of the root (Ginter et al., 2009). Overall, the tooth morphology of *Cladoselache* is similar to that of *Symmoriiformes* and *Ctenacanthiformes*, but the teeth of the latter two taxa are distinguished by the strongly convex labial surface of the median cusp and the absence of triangular projections accompanying the basioblabial depression (Ginter et al., 2009).

In this study, CMNH 8114 was only identified to the genus level. More than 10 species have been identified, mainly by Dean (1909), since the genus *Cladoselache* was first established in 1894. However, his classification needs to be reconsidered because many diagnostic features of the species may have involved taphonomic processes, such as the final resting position in the sediment (Ginter et al., 2009). Taxonomic revisions based on more appropriate morphological features are necessary to enable species-level identification, but this task is beyond the scope of the present study.

DESCRIPTION

Pectoral Girdle and Fins

The pectoral girdle and paired pectoral fins of CMNH 8114 articulated in an almost completely natural position are preserved. The pectoral girdle is dorsoventrally compressed, and only the coracoid region is exposed from the matrix. The coracoid region of the scapulocoracoid consists of two cartilages: the coracoid plate and the procoracoid. The coracoid plate is a triangular cartilage located at the lateroventral margin of the body (Fig. 2B, C). It presents a broad articulation crest for the pectoral fin at its lateral end. The triangular coracoid plate is also found in stethacanthids (*Akmonistion*) (Coates and Sequeira,

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