

Devonian sharks and the origin of Xenacanthiformes

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Abstract

Interrelationships between major groups of Devonian chondrichthyans and the origin of Late Palaeozoic xenacanthiform sharks are considered on the grounds of tooth morphology and biostratigraphy. Suggestion that cladodont-toothed sharks appeared later in the evolution than the diplodont ones is combined with the idea of a phoebodontiform ancestry of xenacanthiforms. Such a phylogenetical model requires the shortest unexplained breaks in stratigraphic record and the lowest morphological barriers between closely related taxa, as far as dentition characters are concerned.

Introduction

Our knowledge of chondrichthyans living prior to the late Famennian, is very modest and based almost entirely on their teeth, scales, and fin spines. Thus far, only five skulls (and/or fragmentary postcranial skeleton) were recorded from the Lower to Middle Devonian: three of apparently only one genus, *Pucapampella* from the Malvinokaffric Realm (Bolivia and South Africa; MAISEY 2001), one of *Antarctilamna*, from the Bunga Beds of New South Wales (Australia; YOUNG 1982), and one of an enigmatic, allegedly toothless shark, *Gladbachus* from Bergisch Gladbach in Germany (HEIDTKE & KRÄTSCHEMER 2001). Skull fragments of three probably different sharks, assigned as '*Cladodus*' *wildungensis*, '*Cladodus*' *hassiacus*, and *Protacrodus vetustus*, were found from the upper Frasnian of Bad Wildungen, Germany (GROSS 1937, 1938). The upper Famennian brings many complete shark skeletons, thanks to the extraordinary preservation of cartilage in the Cleveland Shale of Ohio. However, all of the few hitherto described species (of the genera *Cladoseelache*, *Monocladodus*, *Stethacanthus*, *Tamiobatis*, and *Ctenacanthus*), based on articulated specimens from that area, belong to the same palaeoenvironmental group, i.e. cladodont-toothed surface hunters (WILLIAMS 1990). Therefore, they do not reflect the real diversity of Famennian chondrichthyan faunas. On the other hand, particularly from the time the processing of tons of Devonian rocks in search of conodonts, as useful stratigraphic tools, began in the sixties, thousands of isolated shark teeth were collected. Apart from taxa based on loose teeth from the Cleveland Shale and elsewhere, erected mainly in 19th century and still awaiting revision, there are about 40 already named and probably many more yet undescribed Devonian tooth-based species from all over the world.

Such a disproportion makes it indispensable to seek the relationships between early chondrichthyan taxa not only using more or less articulated specimens in the analyses, but also applying characters of isolated teeth. Unfortunately, such an approach is not widely accepted among the leading palaeoichthyologists. Often there are produced cladograms of early chondrichthyans in which advanced sharks of absolutely different dentitions are grouped together, such as ctenacanth and xenacanthiforms, and in turn, large groups, but known only from teeth, such as phoebodontiforms, are not taken into account at all (e.g., COATES & SEQUEIRA 2001). Of course, anybody who works on chondrichthyan phylogeny should be aware that the teeth are highly adaptive structures and therefore many convergences could, and undoubtedly did, take place during their evolution. However, the example of Xenacanthiformes (= Xenacanthida sensu HAMPE 2003; suffix "-formes" is used for orders following CAPPETTA et al. 1993) indicates that all the representatives of a large group can have the same general type of teeth. Xenacanthiforms are known from the Lower Carboniferous up to the Triassic, from articulated skeletons and characteristic diplodont teeth, i.e. with two lateral cusps evidently larger than the median ones. None of the xenacanth is known

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