

Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity

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Abstract

In terms of diversity and abundance, the two most important groups of Mesozoic elasmobranch fishes are hybodonts and neoselachians (the latter including all the modern sharks and rays). Both groups are probably monophyletic, and hybodonts appear to be the closest extinct sister group to neoselachians. Much of the modern elasmobranch diversity arose in the Mesozoic, and the fossil record suggests that extinction was an important factor in early neoselachian history. The relationships of Mesozoic neoselachians are best investigated within a phylogenetic framework of extant forms. Unfortunately there are significant discrepancies between phylogenetic analyses of modern elasmobranchs founded upon morphological and molecular data. Recently-published morphological trees place the batoids in a terminal position, nested high within squalan sharks. Molecular data from RAG-1 (a nuclear gene) and ND2 (a mitochondrial gene) support an opposite conclusion, in which batoids occupy a basal position as the sister group to modern sharks. Stratigraphic data (heavily biased toward isolated teeth) are highly congruent with the molecular tree, suggesting that the neoselachian fossil record contains only a few gaps of relatively short duration. By contrast the morphological trees predict that numerous lengthy gaps exist in the fossil record of many modern elasmobranch lineages, and that a major radiation of numerous modern elasmobranch lineages occurred prior to the early Jurassic. This is of general interest, because in other phylogenetic studies molecular data have frequently implied greater antiquity than morphological evidence (e.g., mammals, birds). Our findings clearly demonstrate that estimates of taxon longevity are critically dependent on the phylogeny used, and also show how the fossil record may be useful as an arbiter between competing phylogenetic hypotheses.

Introduction

Although several groups of Paleozoic elasmobranchs survived the Permo-Triassic mass extinction, most of these disappeared during the Triassic (including xenacanth, edestids and phoebodontids; MAISEY 1984a, CAPPETTA et al. 1993). Only two elasmobranch lineages, the hybodonts and neoselachians (the latter including all modern sharks and batoids) apparently survived into the Mesozoic (Fig. 1), and only neoselachians continued into the Cenozoic.

Hybodonts were the dominant sharks for much of the Triassic and Jurassic, and include forms several meters in length as well as some of the smallest known sharks (for example the Triassic *Lissodus*, sometimes only a few cm long; ANTUNES et al. 1990). Hybodont dentitions display a range of morphological diversity that probably reflects a wide variety of feeding habits and behavior (MAISEY 1982, 1989), and some taxa were anatomically highly specialized (e.g., *Tribodus*; BRITO & FERREIRA 1989, BRITO 1992, MAISEY & de CARVALHO 1997). Although many hybodonts were marine (e.g., *Hybodus*, *Acrodus*), their remains have also been recovered from Mesozoic non-marine sediments of North and South America, Europe, Africa and Asia, suggesting that some were tolerant of fresh and brackish waters.

Most Mesozoic neoselachians were small (certainly never approaching the size of the largest hybodonts), but the morphological variety of Triassic and Lower Jurassic neoselachian teeth, fin spines and rarer articulated remains suggests these sharks were already highly diversified in marine habitats, although none seems to have colonized fresh waters until the Cretaceous. Several modern neoselachian lineages can be traced back to the Lower and Middle Jurassic, and many more are known from the Upper Jurassic and

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