

# Phylogenetic relationships of the Late Jurassic shark *Protospinax* WOODWARD 1919 (Chondrichthyes: Elasmobranchii)

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## Abstract

Two new specimens of *Protospinax annectans* WOODWARD 1919 are reported. The new material provides an opportunity to re-evaluate the phylogenetic relationships of *Protospinax* in the light of modern cladistic analyses. A revised data matrix, including *Protospinax*, largely extracted from the work of SHIRAI (1992a) is presented. This data matrix contains different interpretations for some of SHIRAI's characters, as well as a few characters not considered by him (pertaining to, e.g., the basihyal and puboischiadic bar). After four iterations of successive weighting, 8 minimum-length trees were found ( $L = 699$  steps,  $c = .60$ ,  $r = .75$ ), of which the strict consensus is very similar to SHIRAI's phylogeny. Squalians share various apomorphic characters, including a basitrabecular process and loss of suborbital shelf (which are also present in *Protospinax*), but the pharyngobranchial blade is best optimized as a galeomorph synapomorphy. Hexanchiformes (including *Chlamydoselachus*) is paraphyletic, but only if *Echinorhinus* is coded as derived for two characters related to the ectethmoid process (as herein re-defined). A character putatively homologous for hexanchiforms (single dorsal fin) was included to further test their monophyly, but this is still not supported. *Protospinax* is resolved as a very derived member of the squalian clade and is the sister-group to Recent hypnosqualeans (a group comprising squatinoids, pristiophoroids and batoids), with which it shares ten apomorphic characters (eight with homoplastic distribution). *Protospinax* retains a basioccipital fovea which is secondarily lost in other hypnosqualeans. An anal fin, basal angle and ectethmoid process are all absent in *Protospinax*, which has ventrally fused coracoids, calcified vertebral centra and an orbital articulation typical of most "orbitostylic" sharks. The phylogenetic position of *Protospinax* is unchanged even when SHIRAI's characters are left unmodified and missing characters in *Protospinax* are excluded from the analysis. Without successive weighting, 252 equally most parsimonious trees ( $L = 163$  steps,  $c = .60$ ,  $r = .75$ ) are produced, all depicting *Protospinax* as a hypnosqualean (forming a basal trichotomy with *Squatina* and the node uniting pristiophoroids and batoids). Although resolution within some higher squalian components varied in our different analyses, *Protospinax* and other hypnosqualeans remained monophyletic. SHIRAI's "hypnosqualean group" is formally recognized as the Superorder Hypnosqualea.

## Introduction

*Protospinax* is the most enigmatic fossil elasmobranch from the Solnhofen Limestone of Bavaria. It has proven to be a controversial and problematical taxon to investigators of elasmobranch relationships. For many years only two specimens were referred to *Protospinax* (WOODWARD 1919), but an additional one was described by MAISEY (1976, also depicted in BARTHEL 1978).

Surprisingly, two magnificent examples have lain unrecognized for more than a century in the Museum of Comparative Zoology of Harvard University. They were purchased by Alexander AGASSIZ from the Häberlein family of Pappenheim (in the early 1880's), as part of a collection of Solnhofen fossils. One had been identified as a *Heterodontus*, the other as *Squatina*. These specimens are much more informative than the already-known examples, and form the basis of the present analysis.

Modern sharks, skates, and rays are united by many synapomorphies and collectively form a mono-

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