

Recognizing paraphyletic stem groups: A case study in the analysis of eubrachythoracid arthrodires (Placodermi)

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Abstract

Studies on the origin and diversity of vertebrates are dependent, in part, upon a clear understanding of the phylogenetic relationships of the organisms under study. However, the use of stem and other paraphyletic groupings is common in the literature. Following the advent of phylogenetic systematics, a clearer picture of phylogenetic relationships emerged. Despite what appeared to be a panacea for phylogenetic debates, a number of questions remain. Among eubrachythoracid arthrodires (Placodermi), the sister groups Coccosteomorphi and Pachyosteomorphi are well established; however, the relationship of basal taxa remains unresolved despite methodological advances. This instability is explained by three hypotheses: (1) a historical artifact in the definition of characters; (2) missing data; and (3) a byproduct of the evolutionary patterns in the groups under study.

Eubrachythoracids are evaluated as a case study to test these hypotheses. Pre- and post-cladistic analyses are reviewed. The use of historically biased characters represents a tautology, a preformed group is used to define a phenetic character and then the character is used to validate the group. Missing taxa (including author's choice) affect character polarity. A study group of taxa should be bounded by outgroups and higher nested taxa otherwise phylogenetic conclusions may be misleading. Missing characters obviously affect a character-based analysis. Evolutionary effects include tempo and the nature of morphological change. Sister taxa with different rates of evolution show different sampling biases. An asymmetrical loss of plesiomorphic characters within one clade results in an increased sensitivity to missing taxa resulting in paraphyly. This scenario is modeled.

The model and a review of eubrachythoracid basal taxa support all three hypotheses, in that each hypothesis explains individual cases. Historical biases and missing data are recognized sources of error; however, evolutionary pattern has been under estimated as an influencing factor. It is predicted that these sources of instability are ubiquitous among phylogenetic analyses. Recognition of the precautions and increased fieldwork portend a fruitful future for our understanding of phylogenetic relationships among arthrodires and other craniate taxa.

Introduction

When considering the origin and early radiation of the vertebrates, analyses either directly or indirectly rely on an understanding of the phylogenetic relationships of the organisms under consideration. Often taken for granted, these hypotheses of relationships may be influenced by their history or underlying assumptions, for example, stem groups, as a concept, are pervasive in the research literature. At a time when the understanding of phylogenetic relationships was unclear, they represented ancestral groups from which descendent lineages were derived. The use of stem group concepts has inertia. Current comparative anatomy texts still continue to refer to mammals as being either derived from reptiles, referred to as mammal-like reptiles, or recognized even as a subgroup of reptiles. This is often compounded by taxonomy where historical group names refer to paraphyletic versus monophyletic groupings (thus the current debate concerning the relationship between taxonomy and systematics, e.g., see NIXON & CARPENTER 2000, and LEE 2001, for a recent exchange).

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