

Structure and implications of theories on the origin of lissamphibians

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Abstract

The origin of the Lissamphibia is the subject of continuing debate, and there is no current consensus. Albeit often considered a different problem, the intrarelationships of crown-lissamphibians have a strong influence on the identification of phylogenetic polarity for the lissamphibian stem, as cladistic reanalyses indicate. Regarding crown-group relationships, there is a majority view that salamanders and anurans are sister groups (Batrachia Hypothesis), supported by morphological and, more recently, molecular studies. The only competing alternative so far generated by molecular systematic analyses is the Procera Hypothesis (salamanders + caecilians). Both albanerpetontids and the stem-groups of the three extant clades contribute significantly to the structure of tree topologies by adding information that often reverses phylogenetic polarity, such as the presence of a stegokrotaphic skull and retention of separate intercentra by *Eocaecilia*.

The major hypotheses of lissamphibian origin (temnospondyl, lepospondyl, and polyphyletic) rely on different character-sets, and true total evidence has not been reached yet. At first sight, the Temnospondyl and Lepospondyl hypotheses appear to involve diametrically opposite interpretations of character evolution, especially regarding the middle ear and vertebral centrum, two character-sets often employed in the study of lissamphibians. Here we discuss the most important among the different sets of characters, analyze their problems and strengths, and test their distribution in the three different phylogenetic topologies. According to this test, most characters can be explained to have evolved equally parsimoniously in the lepospondyl and temnospondyl hypotheses, while the Polyphyletic Hypothesis forms a plausible alternative in only a few cases. While there is some quantitative support in the numerous absence characters (loss of bones) for the Lepospondyl Hypothesis, the evolution of the palate and dentition appears much more plausible (parsimonious) under the Temnospondyl Hypothesis. Surprisingly, vertebral characters do not favour the Lepospondyl Hypothesis, and some of them are well explained by all concepts, including polyphyly.

We conclude that (i) the large number of absence characters is problematic for several reasons while most of them are invalidated by incongruent distribution, (ii) vertebral characters are not decisive at all and their proper understanding requires further studies of development, and (iii) some characters of the middle ear and palate, and dentition appear to be highly informative but are challenged by difficulties in identifying the primitive condition for salamanders. Altogether, our analysis of the palaeobiological implications of the current lissamphibian origin hypotheses favour the Temnospondyl Hypothesis, with the Salientia-Procera Hypothesis of internal relationships involving fewer unparsimonious assumptions than the Batrachia-Gymnophiona Hypothesis.

We suggest that future cladistic analyses will have to deal with a thorough reanalysis of salamander ancestry, total evidence including albanerpetontids, the consideration of ontogenetic changes in morphology in the coding of many character-states, and the inclusion of additional character sources, such as ossification sequences among extant and fossil taxa.

Introduction

The relationships of the three extant groups of amphibians (Anura, Urodela, Apoda) to each other, and the identification of their closest Palaeozoic relatives, have been subjects of controversy over the last century. The interrelationship of the modern groups continues to be controversial because neither morphological nor molecular cladistic analyses give a consistent pattern of relationships between the frogs, salamanders,

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