

Toward a phylogeny of the thelodonts

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Abstract

We investigated the phylogenetic relationships of thelodonts by compiling data on 25 species in 15 genera, comprising most of the known thelodonts represented by articulated specimens (squamations), together with four outgroup taxa. Character states for 53 characters (83 apomorphic states) were compiled and analyzed using Maximum Parsimony methods to yield 150 shortest trees of 177 steps each. The consensus summary of these trees was judged to be unreliable owing to the uncertain placement of two “wild-card” taxa (one of which was an outgroup). After removal of these two taxa a second analysis yielded 31 shortest trees of 153 steps. The consensus tree suggests a monophyletic Thelodonti in which a basal split separates *Phlebolepis* plus *Erepsilepis* and their sister *Archipelepis* from the remaining taxa. Within the remaining species, a group consisting of *Turinia* plus *Loganellia* and their possible sister *Phillipsilepis* is collectively sister to *Shielia* plus *Lanarkia* and their sister the Furcacaudiformes. The latter group is monophyletic and comprises the basal *Pezopallichthys* and a monophyletic Furcacaudidae. These results must be considered tentative pending addition of new characters and inclusion of data from other species of thelodonts.

Introduction

Thelodonts are enigmatic jawless vertebrates from the Paleozoic whose scales are useful for biostratigraphic and paleoenvironmental studies but whose relationships to other early vertebrates remain controversial (JANVIER 1981, 1996, TURNER 1991). In the past two decades, much progress has been made in understanding the body morphology and the distribution of scale types on the bodies of thelodonts that are known from articulated squamations (TURNER 1982, 1991, 1992, MÄRSS 1986, TURNER & VAN DER BRUGGHEN 1993, VAN DER BRUGGHEN 1993, 1994, VAN DER BRUGGHEN & JANVIER 1993, WILSON & CALDWELL 1993, 1998, CALDWELL & WILSON 1995, MÄRSS & RITCHIE 1998, SOEHN et al. 2001, MÄRSS et al. 2002). However, the phylogenetic relationships of individual thelodont taxa have remained largely unresolved, with some authors favoring a monophyletic Thelodonti (e.g., HALSTEAD 1982, FOREY 1984, TURNER 1991) and others suggesting that the group is paraphyletic (e.g., KARATAJUTE-TALIMAA 1978, JANVIER 1981, DONOGHUE & SMITH 2001).

Influential ideas by GROSS (1967) and by KARATAJUTE-TALIMAA (1978) emphasized a division of the Thelodonti into two groups having scale histologies similar either to *Thelodus* or to *Katoporodus*. This two-division idea, modified subsequently by TURNER (1991), who recognized instead four major types, was the foundation for most taxonomic treatments of thelodonts in the late 20th Century.

We suggest that a better way to begin unscrambling the puzzle of thelodont phylogeny is through considering as much information as possible about all of the best-known taxa: those known from articulated squamations, including, wherever possible, information about body morphology, scale morphology, the distribution of scale types on the body, and scale histology. By treating these best-known taxa as individual species in a modern computer-based phylogenetic study, we hoped to begin to group genera and species into monophyletic assemblages and to lay a foundation for testing the monophyly and extra-group relationships of the Thelodonti as a whole.

The relatively new data concerning thelodont anatomy and histology have been obtained both through re-study of some of the earliest described thelodont taxa and through discoveries of new groups of thelodonts. These re-studied and newly discovered fossils all come from northern regions of Europe and

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