

The phylogeny of antiarch placoderms

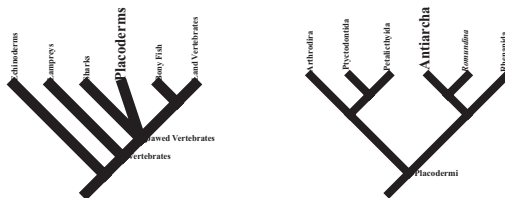
Sarah Kearsley

Abstract

The most comprehensive phylogenetic study of antlarchs to date (Zhu, 1996) included information not derived from observation. In cases where the relevant anatomy was poorly or not at all preserved Zhu sometimes inferred character states from taxa considered to be closely related. These inferences have the potential to affect the topology of the resulting trees. To learn if and how these inferred characters have biased the results several tests have been performed. Heuristic searches for most parsimonious trees were done on Zhu's matrix with and without inferred characters. Bootstrap analysis, Bremer support indices, and the Templeton test were performed on both data sets. The inferred characters were found to increase the robusticity of the results, although they also caused a statistically significantly different tree to be generated. The false resolution and different result suggest that inferring characters does not help the search for accurate phylogenies.

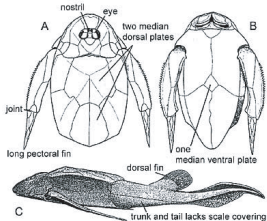
Background

Antiarchs are generally considered to be members of the placodermi, one of the three major branches of jawed vertebrates. Their closest relatives within placoderms are thought to be either the arthrodires or *Romundina*. The cladogram on the right shows Goujet's (1984) phylogeny of the placoderms. The cladogram to the left shows the relationship of placoderms to other vertebrates.



Antiarch anatomy

The identifying characteristics of antiarchs are their long, boxlike thoracic armor and bony jointed pectoral appendages. As in other placoderms, the dermal armor has a higher degree of mineralization than the scales or internal skeleton. For this reason the head, trunk, and pectoral armor are the only parts which are commonly preserved in the fossil record.



The figure to the left is an anatomical diagram of *Bothriolepis* (Ritchie, 2002)

A: Dorsal view

B: Ventral view

C: Lateral view of a reconstruction

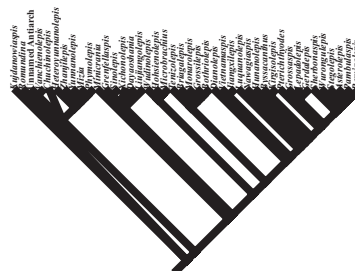
Templeton test

The Templeton test can determine whether or not two apparently different cladograms are actually approximations of the same cladogram. It is a non-parametric Wilcoxon matched-pairs signed ranks test. The number of state changes each character goes through is recorded. The number of changes in one tree are subtracted from those of the other tree. These numbers are the scores. The number of nonzero scores is recorded as n . These scores are assigned a rank based on absolute value. The ranks assigned to positive and negative scores are summed separately. The sum with the smaller absolute value is the Wilcoxon test statistic, T_s . The results are then compared to a table, with a small test statistic indicating a statistically significant result.

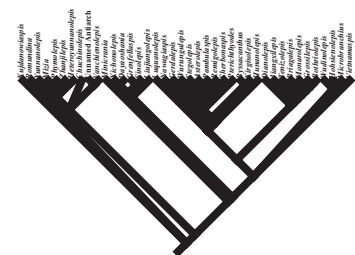
Character	Difference in the number of state changes	Rank	Ts=4	n=8
4	1	4		
5	-1	-4		
12	3	8		
28	1	4		
45	1	4		
51	1	4		
52	1	4		
57	1	4		

For n=8, Ts must be less than or equal to 5 to be significant with 95% confidence. In this case Ts=4, so the two trees are approximations of the same cladogram.

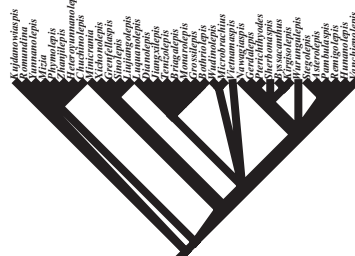
Adams consensus trees



Zhu's published tre



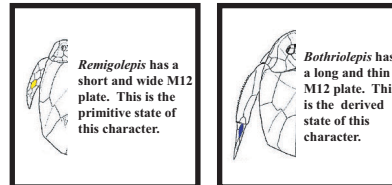
Tree based on Zhu's matrix



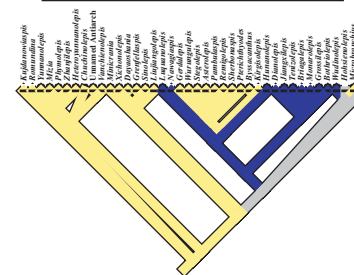
Tree with no inferred character

M12 plate

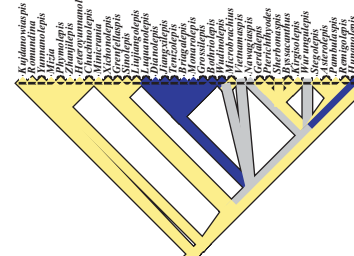
The M12 plate is a small bone in the pectoral appendage. The shape of this bone varies in antiarchs. The evolutionary changes of this character can be traced on the cladograms. In this case, the shape of the plate diagnoses a clade which is only found when inferred characters are omitted.



Legend: ■ M12 plate short ■ M12 plate long ■ Equivocal



Tree based on Zhu's matrix



Tree with no inferred character

Bremer support and bootstrap values

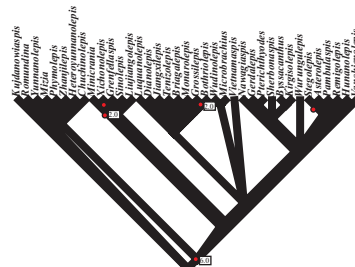
The Bremer support indices and bootstrap percentages both indicate the degree to which the recovered phylogenies are supported by the data. Large Bremer support numbers and bootstrap percentages denote well supported clades. Bootstrap values can also show the accuracy of clades. A clade with a bootstrap value of 70% is accurate with 95% confidence.

In this case, bootstrap values for the two trees do not differ significantly, but some nodes in the tree based on Zhu's matrix have a higher bremer support than the same nodes in the other tree.

In the cladograms below, nodes with bootstrap percentages greater than 70% are marked with a red dot. Bremer support numbers greater than 1.0 are shown to the right of the node.



Tree based on Zhu's matrix



Tree with no inferred character

Conclusion

Zhu's matrix took less time to analyze, and produced a more resolved and more robust result. The added assumptions, however, resulted in a loss of parsimony and potentially a loss of accuracy. the Templeton test demonstrates that it had a statistically significant effect on the resulting cladogram.

Inferred characters in a taxon-character matrix is a bad idea because the added assumptions may cause the recovery of structure not supported by data. In some cases, the tree topology is significantly changed. This has the potential to produce positively misleading phylogenies.

Zhu's published phylogeny should be rejected for another reason as well. The search for most parsimonious trees was not allowed to run to completion. Therefore, Zhu's results are based on only a small fraction of the total number of most parsimonious trees. The differences between the published tree and the newly generated tree reflect this. In this case, the incomplete set of most parsimonious trees caused the monophyly of one of the four major groups of antiarchs to be questioned. Looking at only a small subset of data may be just as misleading as adding assumptions to data.

References

Goujet, D. 1984. Placoderm interrelationships: a new interpretation with a short review of placoderm classifications. *Proceedings of the Linnean Society of New South Wales* 107: 211-243

Ritchie, A. 2002. Palaeontology - Canowindra slide show.
http://www.amonline.net.au/palaeontology/field_sites/slide_show.htm

Zhu, M. 1996. The phylogeny of the Antiarcha (Placodermi, Pisces), with the description of Early Devonian antiarchs from Qujing, Yunnan, China. *Bulletin du Museum National d'Histoire Naturelle* 18: Section C. no. 2-3: 233-347