The phylogeny of antiarch placoderms

Sarah Kearsley
Geology 394 Senior Thesis

Abstract

The most comprehensive phylogenetic study of antiarchs 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.

Table of Contents

Results

Appendices

Matrices

Bremer Support Indices

List of Figures

Introduction

Antiarchs are an early group of jawed fish. They range in age from the Early Silurian to the end of the Devonian, making them some of the earliest known jawed vertebrates. The earliest members of the group are found in China, but later forms are found all over the world.

Most antiarchs lived in fluvial and lacustrine environments, although there are also species which lived in marine environments. They were fairly small in size, the largest being less than a meter in length, and were not streamlined. Most were bottom feeders, and were not fast swimmers.

The identifying characteristics of this group 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.

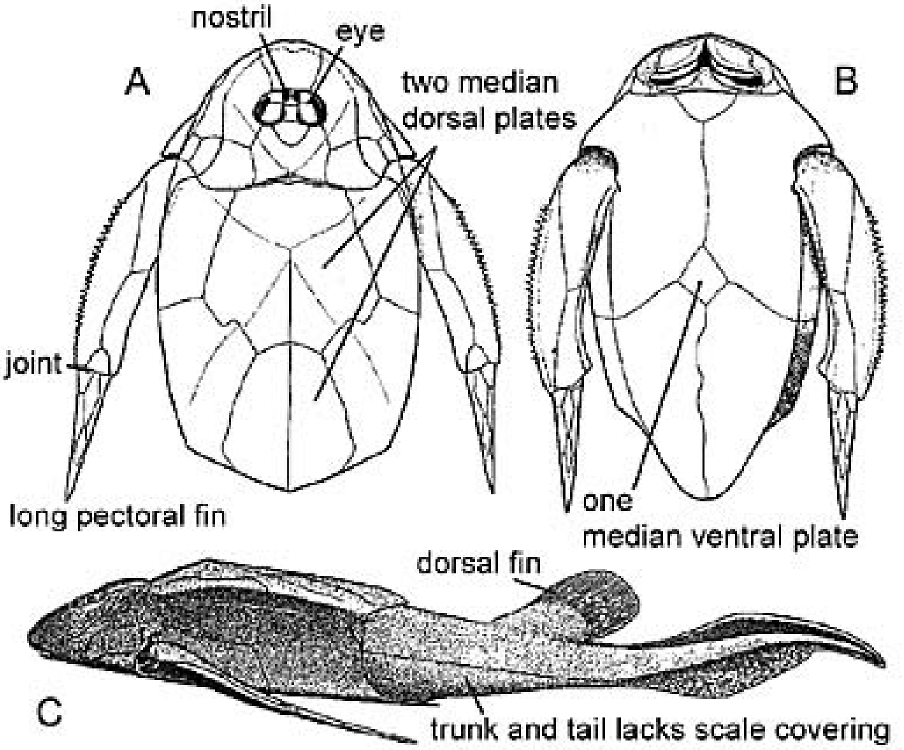

Figure 1: Anatomy of *Bothriolepis* (Image © Alex Ritchie)

Antiarchs are generally considered placoderms, although this has recently been questioned (Johanson, 2002). Placoderms are one of the three major groups of jawed vertebrates, the others being chondrichthys, sharks and other cartilaginous fish, and osteichthys, bony fish and land vertebrates. Unlike other fish, placoderms lack teeth. Instead, they have bony plates to slice or crush food. Their heads and trunks are armored, and in most derived placoderms there is a distinctive joint between the head and thoracic armor. Placoderms had a wide variety of body types and lifestyles, from huge, predatory arthrodires to small, ray-like rhenanids. Placoderms first arose as a minor group in the Silurian, flourished in the Devonian, and then went extinct in the Devonian mass extinction.

Antiarch phylogeny is interesting because it is poorly known and there is some disagreement over it. The traditional classification divides the antiarchs into four subgroups, the Yunnanolepidoidei, the Asterolepidoidei, the Sinolepidoidei, and the Bothriolepidoidei. The yunnanolepidoids are generally considered to be basal to the other antiarchs because they are the oldest members of the group and lack the joint that members of the other groups have in their pectoral appendages. They also have the smallest range, as they are found only in southern China. In contrast, Zhu (1996) found that the bothriolepidoids form a paraphyletic sequence leading to the asterolepidoids and are not the natural group they had been thought to be.

Cladistic methodology has been used to study the phylogenetic relationships of these fish. Cladistics, or phylogenetic systematics, has advantages over other methods of determining phylogeny because all assumptions are made explicit, analyses are repeatable, and statistical tests may be performed on the results. It allows for hypotheses to be favored based on data, not just on the reputation of the systematist.

Observations on anatomical characters or gene sequences are entered into a taxon-character matrix. Character states are generally assigned numbers, with 0 being the primitive state and higher numbers denoting derived states. Cladograms, branching diagrams depicting a phylogenetic hypothesis, are generating using computer algorithms to find the trees which require the fewest possible steps. The shortest trees are the most parsimonious hypotheses of relationship because longer trees require the assumption of more changes.

In cladistic terminology there are three kinds of groups. A polyphyletic group includes members without including a common ancestor. A paraphyletic group consists of an ancestor and some, but not all of its descendants. A monophyletic group, or clade, is one which includes an ancestor and all of its descendants. Monophyletic groups are the least arbitrary, because members are only included or excluded based on phylogeny.

In standard practice, characters are coded solely based on observation. Zhu observed most characters, but in some cases where data were unavailable characters were coded based on assumed close relationships with other taxa. This was done if the character state was stable and uniform in the taxa thought to be most closely related. Inferred characters were then treated in the same manner as observed characters. This was done to lower the number of possible most parsimonious trees, speed the computation time, and allow a more structured tree to be created.

Zhu justifies adding these assumptions on the idea that no set of characters can be objective, so the input in any cladistic analysis is inherently nonobjective. This is true, but why should more assumptions than necessary be added? Zhu gains speed, resolution, and precision, but are the results biased?

Methods and Taxa

Phylogenetic analyses were performed using the matrix created by Zhu and again for the same matrix with inferred characters recoded as missing data.

The published matrix includes 40 ingroup taxa, and 2 outgroup taxa. Of the 44 named genera known at the time 39 were included in the matrix. The remaining five were excluded because their remains were too poorly known. An unnamed antiarch (Janvier, 1995) was also included.

The outgroup taxa are *Kujdanowiaspis* and *Romundina*. *Kujdanowiaspis* is an actinolepid arthrodire, and *Romundina* is an acanthothoracid. Arthrodires and acanthothoracids are the two groups that had been proposed as sister taxa to the antiarchs at the time of publication. (Denison, 1978; Miles and Young, 1977; Goujet 1984).

There are 66 characters in the matrix. These are listed in an appendix. Characters were unweighted and unordered. Zhu did perform an analysis using ordered characters, but the cladogram figured and described in the text was based on an unordered search.

The matrices were compiled in MacClade 3.08a. A Macintosh G4 computer was used, and trees were generated using the heuristic search mode of PAUP 4.0b10. This resulted in large sets of most parsimonious trees, so Adams consensus and agreement subtrees were found.

Ten replicates of the heuristic searches were done. This took as much as 60 hours, so to speed things up, redundant taxa were eliminated from the matrices. Redundant taxa are those which provide no unique information to the matrix. There were more redundant taxa in the matrix from which inferred characters were removed. None of the unique information these genera added was based on observation. Two versions of the original matrix were studied, one with all non-redundant taxa, and one with the same taxon list as the matrix without inferred characters. The topologies of the consensus trees of both versions of Zhu's matrix were identical. *Grossaspis* and *Lepadolepis* were removed from Zhu's matrix. *Dayaoshania*, *Hohsienolepis*, and the unnamed antiarch were redundant in the matrix with no inferred characters.

Results

Description of Trees

Zhu's published tree is 155 steps long and has a consistency index of 48. It is the only tree in which the Bothriolepidoidei is not monophyletic.

The new tree generated from Zhu's matrix is different than the published tree. In the new tree the Bothriolepidoidei and the Sinolepidoidei are monophyletic rather than paraphyletic, although membership in these groups is somewhat different than in the traditional classification. There are several reasons why this may be the case. First, Zhu did not let the search run to completion. Zhu only allowed 100 most parsimonious trees to be saved at any point during the analysis. Instead of continuing and finding more trees, the analysis was cut short. This means that the results Zhu presented were based on only a small subset of the most parsimonious trees. Also, Zhu did not perform search replicates. Repeating searches makes it more likely that the shortest possible trees are found. Ten replicates of the heuristic search in PAUP* were done, and the resulting adams consensus tree, based on 62 most parsimonious trees, is also 155 steps in length. The consistency index of this tree is 48.

Unsurprisingly, there are some differences between consensus trees with and without inferred characters. There were 715 most parsimonious trees. These trees were than the ones derived from Zhu's matrix, at 153 steps. This shortening is most likely due to the lack of information producing a less resolved result. Its consistency index is 48, as in the other trees. When inferred characters are excluded there is a loss of structure, although the four subgroups are still present. *Vanchienoloepis* now falls outside of the Yunnanolepidoidei, and forms a polytomy with the yunnanolepidoids and all other antiarchs. It is not surprising that this taxon becomes less resolved when inferred characters are removed because it had a large number, 11 out of 66, characters inferred. *Vietnamaspis*, *Wurungulepis*, *Wudinolepis*, *Microbranchius*, and *Hunanolepis* also fall out of their groups to form polytomies. Some structure, however, is unique to this tree. *Luquanolepis* becomes a basal member of the Bothriolepidoidei, and *Gerdalepis* and *Pterichthyodes* are sister taxa.

There are observable changes that occur when inferred characters are removed. The tree resulting from a heuristic search is shorter and less resolved in the absence of inferred characters. Also, two navel clades are found when this is done. Simple observation, however, cannot determine how strongly supported these differences are, or if the differences are significant.

Statistical Tests

Three statistical tests were performed on the consensus trees resulting from the cladistic analyses of the two matrices. The bootstrap test and Bremer support index show how well-supported the consensus trees are. The Templeton test can determine if the two trees differ significantly.

The bootstrap analyses were done in PAUP* (Swofford, 1999) using the fast stepwise-addition mode. A bootstrap matrix is created by randomly selecting characters from a taxon-character matrix until the number of characters in the bootstrap matrix is equal to the number of characters in the original matrix. In this case, there were 66 characters in the bootstrap matrices. Random choice results in some characters being chosen multiple times, while other characters are not chosen at all. This has the effect of randomly weighting characters. A heuristic search is then done on the bootstrap matrix to find most parsimonious trees. This is repeated many times. In this case, 100,000 bootstrap matrices are generated from each original matrix. The results of the bootstrap replicates are combined into a majority-rule consensus tree for each original matrix. The degree to which each clade is supported is determined by the percentage of bootstrap trees it appears in. A clade is

considered to be a reflection of the true phylogeny with a 95% accuracy if the bootstrap proportion is above 70% (Hillis and Bull, 1993).

In both trees most of the structure was lost, and what structure was preserved was statistically indistinguishable. The same clades were found to be accurate with 95% confidence. *Sinolepis* and *Grenfellaspis* are sister taxa. *Xichonolepis*, *Grenfellaspis*, *Sinolepis*, and *Liujiangolepis* form a monophyletic group. *Grossilepis* and *Bothrilepisi* are sister taxa. *Asterolepis*, *Pambulaspis*, and *Remigolepis* form a monophyletic group, and in 99-100% of all bootstrap trees Antiarcha is a real group.

Bremer support indices, or decay indices, are another way to gauge the robusticity of the trees. A normal heuristic search only saves the shortest trees. The Bremer support index of a clade is based on longer, less parsimonious trees. The first step in creating a set of indices is to find the shortest possible trees. This is done with a normal heuristic search. The strict consensus of these trees is found. Any branching point, or node, on this tree has a decay index of at least one. A search is then performed for trees with lengths one step longer. Any surviving nodes have a decay index of at least two. This process is repeated until no nodes survive.

Bremer support indices were generated using TreeRot v2 (Sorenson, 1999), a program which creates a command file for PAUP* (Swofford, 1999). This file gives PAUP* a set of constraints which cause it to perform the series of heuristic searches and find the strict consensus trees needed to create decay indices. Twenty replicates are done at each step.

For both data sets most nodes only have a decay index of 1.0. Also, most clades have the same index value whether or not inferred characters are present. Some, however, have a higher index when based on the matrix which includes inferences. No node is more supported when inferences are excluded. The node with the highest index in both sets is the one which defines the Euantiarcha, all antiarchs more derived than the Yunnanolepidoids. Clades and their decay indices are listed in an appendix.

The Templeton test is a statistical test which determines if two cladograms with differing topologies actually represent the same tree within error. 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.

The n value of these two trees is 8, and the test statistic is 4. The maximum test statistic for 95% confidence of difference when n equals 8 is 5. Since T_s is smaller than 5 the hypothesis that the two trees represent approximations of the same tree can be rejected.

Suggestions for Future Work

The addition of inferences to a taxon-character matrix has been shown to affect the cladograms based on that matrix, but that does not mean that their removal has created a cladogram which more closely reflects the true phylogenetic relationships of the group. Zhu's inferences may have been correct. There are two methods by which this may be tested, by comparing phylogeny to stratigraphy, and by adding more data.

The stratigraphic record can influence hypotheses of phylogeny. For example, one of the reasons the yunnanolepidoids are thought to be basal to the rest of the antiarchs is that they are found in older strata. This makes sense because an ancestor should not be younger than its descendant.

This idea is quantified by the stratigraphic consistency index. First appearance data are collected for as many taxa as possible, and are used to determine which nodes are compatible with stratigraphy and which are incompatible. The stratigraphic consistency index is recorded as the ratio of consistent nodes to total nodes.

Due to the incompleteness of the fossil record, stratigraphic ranges are often poorly known. This can decrease the resolution and accuracy of this test. For this reason, stratigraphic consistency can only suggest which hypothesis should be preferred.

Another way to choose between alternate phylogenetic hypotheses is to add more data. The results are likely to change when more characters and taxa are added to the matrix. Would additional data support Zhu's tree or the tree with no inferred characters?

Conclusions

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. It demonstrably had a statistically significant effect on the resulting cladogram.

Inferring characters in a taxon-character matrix is a bad idea because the added assumptions are able to recover structure not supported by data. In some cases, the recovered structure is significantly changed. This has the potential to produce positively misleading phylogenies.

Also, searches for most parsimonious trees are not allowed to run to completion may produce much different results than those which are completed. Looking at only a small subset of data may be just as misleading as adding assumptions to data.

Acknowledgements

Thanks to my advisors, Dr. Holtz and Dr. Merck. Thanks also to Dr. Purdy at the National Museum of Natural History for showing me the Smithsonian's antiarchs.

References

Carr, R. K. 1995. Placoderm diversity and evolution. In: M. Arsenault, H. Lelievre, and P. Janvier. (eds.), Studies on Early Vertebrates (VIIth International Symposium, 1991, Miguasha Parc, Quebec). Bulletin du Museum national díHistoire naturelle, Paris 4e serie, section C 17(1-4) : 85-126

Denison, R. H. 1978. Placodermi. Handbook of Paleoichthyology, Vol. 2, H. P. Schultze. (ed.), Stuttgart: Gustav Fischer Verlag

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

Hillis, D. M. and Bull, J. J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* 42, no. 2:182-192

Janvier, P. 1995. The branchial articulation and pectoral fin in Antiarchs (Placodermi). In: M. Arsenault, H. Lelievre, and P. Janvier. (eds.), Studies on Early Vertebrates (VIIth International Symposium, 1991, Miguasha Parc, Quebec). Bulletin du Museum national díHistoire naturelle, Paris 4e serie, section C 17(1-4) : 143-162.

Johanson, Z. 2002. Vascularization of the osteostracan and antiarch (Placodermi) pectoral fin: similarities, and implications for placoderm relationships. *Lethaia* 35, no. 2:169-186.

Larson, A. 1994. the comparison of morphological and molecular data in phylogenetic systematics. In: Molecular Ecology and Evolution: Approaches and Applications, B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle (eds.) Birkhäuser Verlag Basel/Switzerland

Maddison, D. R. and Maddison, W. P. 1999. MacClade 3.08a

Miles, R. S. and Young, G. C. 1977. Placoderm interrelationships reconsidered in the light of new Ptyctodontids from Gogo, Western Australia. In S. M. Andrews, R. S. Miles, and A. P. Walker. (eds.), Problems in Vertebrate Evolution. Linn. Soc. Symp. Ser. 4: 123-198. London: Academic Press

Sorenson, M. D. 1999. TreeRot, version 2. Boston University, Boston, MA

Swofford, D. L. 1999. PAUP*. Phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sinauer Associates, Sunderland, MA

Templeton, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37 no. 2: 221-244

Young, G. C. 1984. Comments on the phylogeny and biogeography of antiarchs (Devonian placoderm fishes) and the use of fossils in biostratigraphy. Proceedings of the Linnean Society of New South Wales 107: 443-473

(1990. New antiarchs (Devonian placoderm fishes) from Queensland, with comments on placoderm physiology and biogeography. Proceedings of the De Vis symposium Memoirs of the Queensland Museum. 28, no. 1: 35-50

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 díHistoire naturelle 18: Section C. no. 2-3: 233-347

Appendices

Abbreviations

AL	anterior lateral
AMD	anterior median dorsal
Cd1	dorsal central 1
Cd2	dorsal central 2
M1	lateral marginal 1
M12	lateral marginal 12
MxL	mixilateral
PDL	posterior dorsolateral
PL	posterior lateral
PMD	posterior median dorsal
PVL	posterior ventrolateral

Ingroup Taxa

Yunnanolepis
Mizia
Phymolepis
Zhanjilepis
Heteroyunnanolepis
Minicrania
Chuchinolepis
Unnamed Antiarch
Vanchienolepis
Xichonolepis
Grenfellaspis
Dayaoshania
Liujiangolepis
Sinolepis
Luquanolepis
Wudinolepis
Hohsienolepis
Microbranchius
Vietnamaspis
Dianolepis
Jiangxilepis
Tenizolepis
Nawagiaspis
Briagalepis
Monarolepis
Grossilepis
Bothriolepis
Grossaspis
Lepadolepis
Gerdalepis
Wurungulepis
Sherbonaspis
Stegolepis
Byssacanthus
Kirgisolepis
Pterichthyodes
Hunanolepis
Asterolepis
Pambulaspis
Remigolepis

Characters

Characters are discussed in Zhu (1996).

1. Pectoral fin scale-covered (0) or modified into a slender appendage covered with small dermal plates (1)
2. Pectoral fenestra encircled by more than two plates (0) or by a single plate (1).
3. Pectoral fin articulation simple (0), sinolepid type (1), or euantiarch type (2).
4. Axillary foramen small (0) or large (1).
5. Pectoral fin unjointed (0) or jointed (1).
6. Cd1 and Cd2 plates in contact (0) or separated (1).
7. Pectoral fin short (0) or elongated (1).
8. M12 plate relative to the trunk-shield short (0) or long (1)
9. Three (0) or tw0 (1) M1 plates of the distal segment.
10. Trunk shield low and elongate (0) or high and short (1).
11. One (0) or two (1) median dorsal plates.
12. Index between width of anterior margin and maximum width of the AMD plate >55 (0), 35-55 (1), 15-35 (2), or <15 (3)
13. Index between anterior and posterior divisions of the AMD plate <300 (0), 300-500 (1), or >500 (2).
14. Tergal angle of the AMD plate centrally (0) or anteriorly (1) placed.
15. AMD plate completely (0) or partially (1) overlapping the ADL plate.
16. AMD plate underlapping or partly (0) or completely (1) overlapping the PDL (or MxL) plate.
17. AMD plate partly or completely overlapping (0) or underlapping (1) the PDL (or MxL) plate.
18. Anterior ventral process and pit on the AMD present (0) or absent (1).
19. AMD plate without (0) or with (1) the dorsal spine.
20. Lateral process of the PMD plate conspicuous (0) or reduced (1).
21. Crista transversalis interna posterior lying laterally to (0) or behind (1) the posterior ventral pit and process of the PMD plate.
22. Posterior ventral pit and process on the crista transversalis interna posterior (0) or posteriorly migrated behind it.
23. Crista transversalis interna posterior lying laterally to (0) or turning anteriorly and in front of (1) the posterior ventral process and pit.
24. Presence (0) or loss (1) of the AL plate.
25. Absence (0) or presence (1) of Changís apparatus.
26. Absence (0) or presence (1) of of the ventrolateral fossa of the trunk-shield.
27. PDL and PL plates independent (0) or fused to form a MxL plate (1).
28. PVL and PL plates independent (0) or fused to form (or replaced by) a single plate (1).
29. Semilunar plate paired (0) or unpaired (1).
30. Absence (0) or presence (1) of a large rectangular aperture on the ventral wall of the trunk shield.
31. Presence (0) or absence (1) of the spinal plate.
32. Postbranchial lamina external and upright (0) or internal and horizontal (1).
33. Adult ornamentation tubercular (0) or reticular (1).
34. Adult ornamentation tubercular (0), ridged (1), or subparallel ridges on the dorsal wall of the trunk-shield.
35. Absence (0) or presence (1) of ridged scales.
36. Absence (0) or presence (1) of a dorsal spongy layer in the dermal bone of the trunk-shield.
37. Presence (0) or absence (1) of the central sensory line groove.
38. Presence (0) or absence (1) of the supraorbital groove.
39. Presence (0) or absence (1) of X-shaped pit-line grooves.
40. Presence (0) or absence (1) of the branch of the infraorbital groove diverging on lateral plate.
41. Absence (0) or presence (1) of the semicircular pit-line groove.

42. Middle pit-line groove issued from the infraorbital groove absent or short (0) or long and extending onto the nuchal plate (1).
43. Absence (0) or presence (1) of the lateral plate.
44. Absence (0) or presence (1) of the premedian plate.
45. Preorbital depression present (0) or absent (1).
46. Preorbital depression extending laterally onto the lateral plates (0) or restricted to the premedian plate (1).
47. Preorbital recess absent (0), restricted tot he premedian plate (1), or extending laterally to the lateral plates (2).
48. Orbital opening open (0) or enclosed by dermal skull roof plates (1).
49. Nasal opening at the anterolateral corners of the rostral plate (0) or at the anterior margin of the rostral plate (1).
50. Narrow (0) or broad (1) lateral plate.
51. Premedian plate short and broad (0) or long and narrow (1).
52. Anterior margin of the premedian plate convex (0) or slightly concave (1).
53. Absence (0) or presence (1) of an unornamented shelf and rostrocaudal groove on the premedian plate.
54. Rostral width/orbital width index of the premedian plate smaller (0) or larger (1) than 200.
55. Orbital fenestra large (0) or small (1).
56. Relative position of the orbital fenestra anterior (0), alightly anterior (1), slightly posterior (2), or posterior (3).
57. Postpineal and nuchal plate long and narrow (0) or short and broad (1).
58. plate without (0) or with (1) orbital fenestra.
59. Long (0) or short (1) obstantic margin.
60. Absence (0) or presence (1) of the submarginal articulation.
61. Endocranial postorbital process short (0) or extending in front of the orbital notch (1).
62. Absence (0) or presence (1) of pronounced postpineal thickening.
63. Presence (0) or loss (1) of the prelateral plate.
64. Prelateral plate with long anterior process (0) or equilateral, triangular in shape (1).
65. Prelateral plate behind (0) or above (1) the mental plate.
66. Mental plate of both sides separated (0) or meeting in the midline (1).

Matrices

Zhu's matrix with redundant taxa removed

```
         10        20        30        40        50        60      }
Kujdanowiaspis
00???????000????????000000000000000000000000???0???????0?0000?0100
Romundina
00???????100????????00000000?1000000000000010?000?000000001?00??0?
Yunnanolepis
11000000?01300000000001111000??100?010000011000101000010000000???0
Mizia
11000000?0130000000000100100001100?0111000110001010000000000000000
Phymoleis
11000000?0130000000000101100001100?0110000110001010000000000000???0
Zhanjilepis
11000000?0130000000000010100001100?0100000111?2101000000000000????
```

```
Heteroyunnanolepis
11000000?013000000000001000000110000??????11???10??00??????000????
Minicrania
11000000?0100100000000010000001100?010110111001100000000000000???0
Chuchinolepis
11000000?0130100000000010000001100?0100000110001010000100000000????
Unnamed_Antiarch
11000000?01???0?0000???1000?011100?0??????11???10??00??????000????
Vanchienolepis
1101?0?0?01301000100???10000011100?0??????11???10??00??????000????
Xichonolepis
111010?000121101000001010001011100?01111001101?101000111000000????
Grenfellaspis
111010?000112101000101010001011100?011110011011101000110000000????
Dayaoshania
111010000012110100000??10001011100?01111001101?101000110100000????
Liujiangolepis
111010100010010100000??10001011100001111001100?101000112100000????
Sinolepis
111010?00010210100010??10001011100?01111001101?100000110000000????
Luquanolepis
11201?01?011010??00010010000101100?0?1????11???10??00?????????????
Wudinolepis
11211?01?0100100100010010001101101?00111011100?1011000030?0?00????
Hohsienolepis
112?1?0??0100100100010010001101102?001110?1100?101100003000??0????
Microbrachius
11211?00?0100100100010010001101102?001110111000101100003000100????
Vietnamaspis
11211????0110100100110010001101100?0?1????000??10?10000???????????
Dianolepis
1120100??0110100100010010001101100?0011100111?2101100002100100????
Jiangxilepis
11211011?0110100111010010001101110?0111100111?2100100002100?00????
Tenizolepis
112?1??1?0100110100010010001101100?011?10?111?2101100002100???????
Nawagiaspis
11201????11101???00010010000101100?011??00111??1001000031??1000010
Briagalepis
112?1????0100110100010010001101100?011100?11???10??00????1?1??????
Monarolepis
112011???0100110100010010001101100?0011???11???10??00?????????????
Grossilepis
1121111110100101000010010001101100?0010010111?2101100012110110011?
Bothriolepis
112111111010010010001001000110111000010010111?21011000121101100110
Gerdalepis
1120100001110000110010010010101100?1111101111?1100000000001???1???
Wurungulepis
11201000?11?00001?001001000000110010?1????11???10???0?????????????
```

```
Sherbonaspis
1120100001120000110010010010001100?0111??0000?110001000?1010001???
Stegolepis
11201000?112000001101001000000110??0111101111?1100110001101???1???
Byssacanthus
11201000111100000110100100?0001100?0111111111?11001000020010001???
Kirgisolepis
11201????11100????1010010010?01100?0010011111?1100100002101???1???
Pterichthyodes
112010000111000011001001001000110010110101111?11001000021010001??1
Hunanolepis
1120100111110000110010010010001100?0111101111?11001000031010001???
Asterolepis
112010001013000101001001001000110010111101111?11100110011010001??1
Pambulaspis
1120?000?0130000110010010000001100?0111101111?1110011001101?011???
Remigolepis
11200000?0130000010010010000001100?0111101111?11100110011010011??1
```

Zhu’s matrix with redundant taxa and inferred characters removed

```
        10        20        30        40        50        60      ]
Kujdanowiaspis
00???????000????????000000000000000000000000???0???????0?0000?0100
Romundina
00???????100????????00000000?1000000000000010?000?000000001?00??0?
Yunnanolepis
1100?0?0?01300000000001111000??100?010000011000101000010000000???0
Mizia
1100?????0130000000000100100001100?0111000110001010000000000000000
Phymoleis
1100?0?0?0130000000000101100001100?011000011000101000000000000???0
Zhanjilepis
1100?????0130000000000010100001100?0100000111?2101000000000000????
Heteroyunnanolepis
1100?????013000000000001000000110000??????????????????????????????
Minicrania
1100?????01001??0000000100000011 00?010110111001100000000000000???0
Chuchinolepis
1100?0?0?0130100000000010000001100?010000011000101000010000000????
Vanchienolepis
1101?????0130100010 0???1000001110 0?0??????????????????????????????
Xichonolepis
11101??0?01211010000010100010111 00?01111001101?101000111000000????
Grenfellaspis
1110???0?0112101000101010001011100?01111001101110100011 0000000????
Liujiangolepis
11?010100010010100000??10001011100001111001100?1010001121 00000????
```

```
Sinolepis
11??10?0?010210100010??10001011100?01111001101?10000011000000????
Luquanolepis
11201?01?011010??00010010000101100?0??????????????????????????????
Wudinolepis
11211?01?0100100100010010001101101?0011101110 0?101100003 0?0?00????
Microbrachius
11211?00?0100100100010010001101102?0011101110001011000030001 00????
Vietnamaspis
1121????0110100100110010001?01100?0??????000??1??1?000???????????
Dianolepis
1120100??0110100100010010001101100?0011100111?2101100002100100????
Jiangxilepis
1121101 1?0110100111010010001101110?0111100111?2100100002100?00????
Tenizolepis
112?1??1?0100110100010010001101100?011?10?111?2101100002100??????
Nawagiasp is
1120????11101???00010010000?01100?01???00111??1001000031??1000010
Briagalepis
112??????0100110100010010001?01100?011100?11???1?????????1?1??????
Monarolepis
1120?1???0100110100010010001101100?0011???11???10??00?????????????
Grossilepis
112111111010010100001001000110110 0?0010010111?2101100012110110011?
Bothriolepis
1121111110100100100010010001101110000100101 11?2101100012110110011 0
Gerdalepis
1120100001110000110010010010101100?1111101111?11000000000001???1???
Wurungulepis
1120?????11?00001?0????100?0??110010??????????????????????????????
Sherbonaspis
11201???0112000011001001001 0?01100?01?1??0000?110001000?101000 1???
Stegolepis
1120?????1120000011010010000000110??0111101111?1100110001101???1???
Byssacanthus
11201000111100000110100100?0001100?0111111111?1100100002001000 1???
Kirgisolepis
1120?????11100????1010010010?01100?0010011111?1100100002101???1???
Pterichthyodes
112010000111000011001001001000110010110101111?11001000021010001??1
Hunanolepis
1120100111110000110010010010001100?01111011 11?1100100003101000 1???
Asterolepis
112010001013000101001001001000110010111101111?1110011001101000 1??1
Pambulaspis
11???????0130000110 0???10000??1100?0111101111?1110011001101?011???
Remigolepis
1120000 0?0130000010010010000001100?0111101111?1110011001101001 1??1
```

Bremer support indices

Zhu’s matrix

```
Mizia, Phymoleis
   156.0             1.0
Yunnanolepis, Mizia, Phymoleis
   156.0             1.0
Yunnanolepis, Mizia, Phymoleis, Zhanjilepis
   156.0             1.0
Yunnanolepis, Mizia, Phymoleis, Zhanjilepis, Heteroyunnanolepis
   156.0             1.0
Unnamed_Antiarch, Vanchienolepis
   156.0             1.0
Yunnanolepis, Mizia, Phymoleis, Zhanjilepis, Heteroyunnanolepis, Chuchinolepis, Unnamed_Antiarch,
Vanchienolepis
   156.0             1.0
Xichonolepis, Dayaoshania
   156.0             1.0
Grenfellaspis, Sinolepis
   156.0             1.0
Xichonolepis, Dayaoshania, Grenfellaspis, Sinolepis
   156.0             1.0
Xichonolepis, Dayaoshania, Grenfellaspis, Sinolepis, Liujiangolepis
   157.0             2.0
Pambulaspis, Remigolepis
   156.0             1.0
Asterolepis, Pambulaspis, Remigolepis
   158.0             3.0
Stegolepis, Asterolepis, Pambulaspis, Remigolepis
   156.0             1.0
Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis
   156.0             1.0
Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis
   156.0             1.0
Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis
   156.0             1.0
Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes
   156.0             1.0
Byssacanthus, Kirgisolepis
   156.0             1.0
Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes,
Byssacanthus, Kirgisolepis
   156.0             1.0
Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes,
Byssacanthus, Kirgisolepis, Hunanolepis
```

158.0 3.0

Nawagiaspis, Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes, Byssacanthus, Kirgisolepis, Hunanolepis

156.0 1.0

Luquanolepis, Nawagiaspis, Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes, Byssacanthus, Kirgisolepis, Hunanolepis

156.0 1.0

Grossilepis, Bothriolepis

157.0 2.0

Monarolepis, Grossilepis, Bothriolepis

156.0 1.0

Briagalepis, Monarolepis, Grossilepis, Bothriolepis

156.0 1.0

Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis

156.0 1.0

Luquanolepis, Nawagiaspis, Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes, Byssacanthus, Kirgisolepis, Hunanolepis, Wudinolepis, Hohsienolepis, Microbrachius, Vietnamaspis, Dianolepis, Jiangxilepis, Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis

158.0 3.0

Xichonolepis, Dayaoshania, Grenfellaspis, Sinolepis, Liujiangolepis, Luquanolepis, Nawagiaspis, Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes, Byssacanthus, Kirgisolepis, Hunanolepis, Wudinolepis, Hohsienolepis, Microbrachius, Vietnamaspis, Dianolepis, Jiangxilepis, Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis

156.0 1.0

Minicrania, Xichonolepis, Dayaoshania, Grenfellaspis, Sinolepis, Liujiangolepis, Luquanolepis, Nawagiaspis, Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes, Byssacanthus, Kirgisolepis, Hunanolepis, Wudinolepis, Hohsienolepis, Microbrachius, Vietnamaspis, Dianolepis, Jiangxilepis, Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis

156.0 1.0

Yunnanolepis, Mizia, Phymoleis, Zhanjilepis, Heteroyunnanolepis, Chuchinolepis, Unnamed_Antiarch, Vanchienolepis, Minicrania, Xichonolepis, Dayaoshania, Grenfellaspis, Sinolepis, Liujiangolepis, Luquanolepis, Nawagiaspis, Gerdalepis, Wurungulepis, Stegolepis, Asterolepis, Pambulaspis, Remigolepis, Sherbonaspis, Pterichthyodes, Byssacanthus, Kirgisolepis, Hunanolepis, Wudinolepis, Hohsienolepis, Microbrachius, Vietnamaspis, Dianolepis, Jiangxilepis, Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis

163.0 8.0

Zhu's matrix with inferred characters removed

Mizia, Phymoleis

154.0 1.0

Yunnanolepis, Mizia, Phymoleis

154.0 1.0

Yunnanolepis, Mizia, Phymoleis, Zhanjilepis

```
   154.0            1.0
Yunnanolepis, Mizia, Phymoleis, Zhanjilepis, Heteroyunnanolepis
   154.0            1.0
Grenfellaspis, Sinolepis
   154.0            1.0
Xichonolepis, Grenfellaspis, Sinolepis
   154.0            1.0
Xichonolepis, Grenfellaspis, Sinolepis, Liujiangolepis
   155.0            2.0
Grossilepis, Bothriolepis
   155.0            2.0
Monarolepis, Grossilepis, Bothriolepis
   154.0            1.0
Briagalepis, Monarolepis, Grossilepis, Bothriolepis
   154.0            1.0
Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis
   154.0            1.0
Byssacanthus, Kirgisolepis
   154.0            1.0
Pambulaspis, Remigolepis
   154.0            1.0
Asterolepis, Pambulaspis, Remigolepis
   154.0            1.0
Gerdalepis, Wurungulepis, Sherbonaspis, Stegolepis, Byssacanthus, Kirgisolepis, Pterichthyodes, Hunanolepis,
Asterolepis, Pambulaspis, Remigolepis
   154.0            1.0
Nawagiaspis, Gerdalepis, Wurungulepis, Sherbonaspis, Stegolepis, Byssacanthus, Kirgisolepis, Pterichthyodes,
Hunanolepis, Asterolepis, Pambulaspis, Remigolepis
   154.0            1.0
Luquanolepis, Wudinolepis, Microbrachius, Vietnamaspis, Dianolepis, Jiangxilepis, Tenizolepis, Briagalepis,
Monarolepis, Grossilepis, Bothriolepis, Nawagiaspis, Gerdalepis, Wurungulepis, Sherbonaspis, Stegolepis,
Byssacanthus, Kirgisolepis, Pterichthyodes, Hunanolepis, Asterolepis, Pambulaspis, Remigolepis
   154.0            1.0
Yunnanolepis, Mizia, Phymoleis, Zhanjilepis, Heteroyunnanolepis, Minicrania, Chuchinolepis, Vanchienolepis,
Xichonolepis, Grenfellaspis, Sinolepis, Liujiangolepis, Luquanolepis, Wudinolepis, Microbrachius,
Vietnamaspis, Dianolepis, Jiangxilepis, Tenizolepis, Briagalepis, Monarolepis, Grossilepis, Bothriolepis,
Nawagiaspis, Gerdalepis, Wurungulepis, Sherbonaspis, Stegolepis, Byssacanthus, Kirgisolepis, Pterichthyodes,
Hunanolepis, Asterolepis, Pambulaspis, Remigolepis
   159.0            6.0
```