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The phylogeny of the ‘higher’ temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli

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A parsimony analysis of ‘higher’ temnospondyls (all temnospondyls descended from the common ancestor of *Eryops* and *Parotosuchus*) was performed using 37 terminal taxa and 121 osteological characters. Bremer support values for each internal node were calculated as a measure of clade strength. Additionally, the shortest trees that conformed to some alternative hypotheses were searched for. The following new taxa are established on the basis of the results: Euskelia (the clade containing the Eryopoidea and Dissorophoidea), Limnarchia (the clade containing Trimerorhachidae, Dvinosauroidea, Archegosauroidea and Stereospondyli), Dvinosauria (the clade containing Trimerorhachidae and Dvinosauroidea), Stereospondylomorpha (the clade containing Archegosauroidea and Stereospondyli), Capitosauria (the clade containing *Lydekkerina* and ‘capitosauroids’), and Trematosauria (the clade containing Trematosauroidae, Rhytidosteidae, Plagiosauroidae, Metoposauroidea and Brachyopoidea). The monophyly of the assemblage of Mesozoic families called the Stereospondyli by Romer is supported. The dominance of the Stereospondyli in the Mesozoic and its rarity in the Palaeozoic is discussed. It is suggested that the radiation of the diverse stereospondyl clades, the Capitosauria and Trematosauria, began in the Late Permian of Gondwana, in a ‘safe haven’ that was less severely affected by the Late Permian extinction event. It is further speculated that the ‘safe haven’ was located in Antarctica, or possibly Australia.

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ADDITIONAL KEY WORDS:—phylogenetic – Temnospondyli – Gondwana – Permian – Triassic – Palaeozoic – Mesozoic.

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INTRODUCTION

Apart from the extant Lissamphibia and Amniota, the only clade of terrestrial vertebrates to survive into the Late Triassic and beyond, was the Temnospondyli. Usually regarded as early amphibians (e.g. Milner, 1990b; Trueb & Cloutier, 1991; Coates, 1996), recent research suggests that they lie outside of the tetrapod crown clade (Laurin & Reisz, 1997). Thus they do not belong to the Amphibia, which is defined as a stem-based taxon of crown group tetrapods more closely related to Lissamphibia than to Amniota. The Temnospondyli were a diverse clade amongst the higher level taxa of Palaeozoic terrestrial vertebrates but despite the significance of this clade the interrelationships within it remain poorly resolved at best.

A number of phylogenetic hypotheses regarding the ingroup relationships of temnospondyls, or part thereof, have been published. Nevertheless most of these use a restricted number of terminal taxa covering a limited subset of temnospondyl diversity, the 'trimerorhachoids' being covered by Coldiron (1978) and Foreman (1990), the 'eryopoids' by Boy (1990, 1993) and Milner (1990a), the Dissorophoidea by Daly (1994), and Mesozoic temnospondyls by Warren & Black (1985). The only truly comprehensive phylogenetic hypothesis of temnospondyl interrelationships is that of Milner (1990b), which contained 37 terminal taxa, including both Palaeozoic and Mesozoic forms. Unfortunately no data matrices were provided for any of these analyses, though character state changes for each character were mapped onto the cladograms of Boy and Warren & Black. Furthermore these analyses were performed 'by hand', thus it is not possible to assess whether the topologies presented are the parsimonious solutions. In effect the hypotheses remain untested (Smith, 1994).

To date there are only three published, computer based, parsimony analyses covering a range of temnospondyls. That of Damiani & Warren (1996) dealt with the relationships of the Brachyopidae, and the analysis included a limited number of characters and few taxa outside of the Brachyopoidea and the Dvinosauroidea, thus constraining the Brachyopoidea to fall within the Dvinosauroidea. Similarly the analysis of Trueb & Cloutier (1991) was restricted in that it was primarily concerned with the origins of the Lissamphibia. They included few temnospondyls outside of the Dissorophoidea, a group that they thought contained the ancestor of the lissamphibians. Their analysis contains little information about temnospondyl phylogeny beyond the ingroup relations of the Dissorophoidea. The analysis of Holmes, Carroll & Reisz (1998) included a moderate range of early temnospondyls. Since the aim of their work was to place the basal *Dendrerpeton* in a phylogenetic framework, no Mesozoic temnospondyls were included. Our work focuses on the later temnospondyl taxa and compliments the analysis of Holmes *et al.* (1998).

This study aims to fill the gap in the studies of temnospondyl phylogeny by performing a computer based parsimony analysis on a large data matrix, sampling the full range of temnospondyl diversity above the basal forms and including as many characters as possible.

DEFINITION OF THE TEMNOSPONDYLI

Although this analysis is concerned with the phylogenetic relationships of temnospondyls above such basal taxa as Colosteidae, Edopoidea and *Dendrerpeton*, it

is worth digressing to discuss exactly what a temnospondyl is. The content of Temnospondyli has changed greatly since it was originally proposed by Zittel (1888). Romer (1947) reviewed the changes in classification up to that date. Since then the taxon Temnospondyli has come to include rhachitinous basal tetrapods with large interpterygoid vacuities, typified by such forms as *Eryops*, *Trimerorhachis* and various Mesozoic stereospondyls. There is little to be gained by applying a phylogenetic definition of the Temnospondyli that greatly upsets the modern concept of what is and what is not a temnospondyl. It is unfortunate that when defining the Temnospondyli, de Queiroz & Gauthier (1992) did not do so with respect to any accepted temnospondyl. The Temnospondyli was defined as a stem-based taxon including all tetrapods more closely related to modern amphibians than to the Amniota. This works well if the underlying hypothesis, that the traditional temnospondyls include the ancestors of the Lissamphibia, holds true. However this hypothesis had not been rigorously tested at the time. Laurin & Reisz (1997) have since performed a large parsimony analysis using a range of Lissamphibia, Amniota and Palaeozoic Choanata. They found that it was the Lepospondyli and not the Temnospondyli that included the ancestors of the Lissamphibia. The Temnospondyli was found to occupy a position outside the tetrapod crown clade. Carroll (1995) also found by parsimony analysis that the Lepospondyli and Amniota are more closely related to each other, than either is the Temnospondyli. Only Palaeozoic taxa were included by Carroll so the position of the Lissamphibia was untested. If de Queiroz & Gauthier's definition is employed, and Laurin & Reisz's phylogeny is accepted then we are left with a Temnospondyli that does not include any traditional temnospondyls but, instead, includes the Lepospondyli, a group which have never in the past been included in the Temnospondyli. In situations such as this, we doubt the value of applying strict priority to phylogenetic definitions as proposed by Padian & May (1993). To maintain stability in the content of Temnospondyli, we advocate that de Queiroz & Gauthier's definition of the taxon be abandoned. Instead, we propose that Temnospondyli be defined as a stem-based taxon including all choanates more closely related to *Eryops* than to *Pantylus* (Microsauria). By defining the temnospondyls with respect to Microsauria the group composition remains relatively insensitive to the large scale differences in topology between competing hypotheses of early tetrapod phylogeny.

MONOPHYLY OF THE INGROUP

The ingroup of this analysis comprises the 'higher temnospondyls', which has been defined as all descendants of the common ancestor of the eryopid-dissorophoid group and the stereospondyl group (effectively the common ancestor of *Eryops* and the capitosaurid, *Parotosuchus*, and all of its descendants) (Milner, 1990a). Most previous hypotheses (e.g. Milner, 1990a, b; Sequeira & Milner, 1993; Milner & Sequeira, 1994) have regarded *Trimerorhachis* and related forms to fall outside this group. Nevertheless *Trimerorhachis* possesses several character states that suggest it is nested within the higher temnospondyls, so it is included in our analysis. *Balanerpeton*, *Dendrerpeton*, Edopoidea and Colosteidae are successive outgroups. The ingroup can be diagnosed by the following two synapomorphies:

- (1) Loss of the entepicondylar foramen. The humerus of Colosteids, *Dendrerpeton* and

Balanerpeton has a large foramen passing from the dorsal to the ventral side of its distal end, in the vicinity of the entepicondyle. No such foramen is present in any member of the ingroup for which a humerus is known. An isolated humerus, lacking the entepicondylar foramen was referred to *Edops* by Romer & Witter (1942). If this identification is correct (and it does seem likely) then *Edops* would have developed the derived condition independently of the ingroup.

(2) Posterior coronoid is visible when the mandible is viewed laterally. In all members of the outgroup the dorsal margin of the mandible is relatively straight in lateral view and the posterior coronoid is restricted to the medial side. In most members of the ingroup the posterior end of the posterior coronoid is expanded laterally and dorsally contributing to a coronoid process which can be seen laterally. The size and height of the coronoid process is quite variable and it is sometimes not present at all (e.g. *Lapillopsis* and *Capitosauridae*). Nevertheless the posterior coronoid can still be seen on the dorsal margin, posterior to the dentary tooththrow, when the mandibles of these taxa are viewed laterally. *Trimerorhachis* displays the plesiomorphic condition which is interpreted as a reversal.

MATERIAL AND METHODS

A taxon-character matrix was compiled using 37 terminal taxa (Table 1) and 121 osteological characters (Appendix 1). Some characters that had not been previously used in any systematic work were employed (characters 16, 19, 22, 43, 55, 64, 69, 85, 88, 97, 98, 99, 112, 113, 116 and 121), and the rest obtained from the literature. Continuously variable characters were broken into discrete character states by plotting as many examples as could be gleaned from the ingroup (or related genera not actually included in the analysis) on a frequency histogram. Character state changes were then set using breaks between distribution peaks. Multistate characters were ordered when they obviously represented stages of a transformation series (characters 14, 17, 18, 28, 34, 40, 48, 63, 68, 76, 78, 95, 101 and 105), otherwise they were left unordered.

Character polarities were determined by comparison with four serially closer outgroups. These were *Greererpeton*, *Edops*, *Dendrerpeton*, and *Balanerpeton*. The position of *Edops*, *Dendrerpeton* and *Balanerpeton* follows the phylogenetic hypotheses of Milner (1990b), Sequeira & Milner (1993), Milner & Sequeira (1994), and Holmes *et al.* (1998). The colosteid *Greererpeton* was selected as the most distant outgroup following the phylogenetic hypotheses of Carroll (1995) and Laurin & Reisz (1997). These analyses find that colosteids and all other temnospondyls form a clade that is on the tetrapod stem. Milner (1990b) preferred the hypothesis that microsaurians are more closely related to temnospondyls than colosteids are. The analysis of Laurin & Reisz (1997) is preferred here because it is the only one to include a range of lepospondyls, temnospondyls and lissamphibians and thus did not constrain the position of temnospondyls with respect to other groups.

To reduce *a priori* assumptions of monophyly at the family level, generic level terminal taxa were used as much as possible. Nevertheless in many instances single genera, from families whose monophyly is well supported, are not represented by complete material. In these cases the family was used as a terminal taxon by combining complimentary information from two or more genera. The exception is

TABLE 1. Terminal taxa used in this analysis and the specimens and literature from which the data was gathered. A (c) behind a specimen number indicates only a cast of the specimen was examined

Terminal taxa	Specimens	Literature
<i>Isodectes obtusum</i>	USNM 4471 (c), AMNH 2455, 6928, 6934	Watson, 1956
<i>Acroploous vorax</i>		Coldiron, 1978; Foreman, 1990
<i>Tupilakosaurus</i> spp.	PIN 1025/1, 1255/30, 1025/66, MGUH VP3328, 3329.	Nielsen, 1954; Shishkin, 1973
Undescribed genus	UCMP 42777, 42778, 42780, 42781	Warren, submitted
<i>Dvinosaurus primus</i>		Shishkin, 1973; Nikitin, 1995
<i>Trimerorhachis</i> spp.	AMNH 4565, 4720, 4763, 23625, MCZ 3221.	Williston, 1915; Case, 1935; Berman & Reisz, 1980
<i>Neldasaurus wrightae</i>		Chase, 1965
<i>Sclerocephalus</i> spp.		Boy, 1988; Meckert, 1993; Werneburg, 1992
<i>Cheliderpeton latirostre</i>		Boy, 1993
<i>Archegosaurus decheni</i>	NMV P198456, 198458, 198459, 24165, 274666	Meyer, 1857; Jaekel, 1896; Gubin, 1997
<i>Platyoposaurus stuckenbergi</i>		Gubin, 1991
<i>Könzhukovia vetusta</i>		Gubin, 1991
<i>Pellobatrachus pustulatus</i>		Panchen, 1959
Rhinesuchidae		Hoepen, 1915; Watson, 1962
<i>Lappillopsis nana</i>	QM F12284, 12285, 12289, 14497, 14499, 14501, 14502, 14504–1451	Warren & Hutchinson, 1990
<i>Lydekkerina huxleyi</i>	UCMZ T221	Parrington, 1948; Shishkin, Rubidge & Kitching, 1996
Capitosauridae	QM F6571, 10114, 12281, 12282, 12290–12292, 14481	Watson, 1958; Howie, 1970; Warren, 1980, Warren & Hutchinson, 1988
<i>Mastodonsaurus giganteus</i>		Fraas, 1889; Wepfer, 1923;
<i>Benthosuchus sushkini</i>		Bystrow & Efremov, 1940
<i>Luzocephalus</i> spp.	PIN 3784/1 (c)	Säve-Söderbergh, 1935; Shishkin, 1980
<i>Almasaurus habbazi</i>	MNHN ALM42 (c), 43, 44, 45, 51, 62, 65	Dutuit, 1976
<i>Buettneria perfecta</i>	AMNH 7521, 7721, MCZ 1054, 1056	Sawin, 1945; Hunt, 1993
<i>Laidleria gracilis</i>	AIM F4313	Warren, 1998
Plagiosauridae	SMNS 56614, Undescribed Greenland material at MCZ	Nilsson, 1946a; Shishkin, 1987; Warren, 1995
<i>Xenobrachyops allos</i>	QM F6572	Howie, 1972; Damiani & Warren, 1996
<i>Batrachosuchus</i> spp.	WAM 62.1.42, UCMP 42856, 80859, 80860, 140580, 140583*.	Watson, 1956; Cosgriff, 1969; Chernin, 1977; Warren & Marsicano, in press
<i>Siderops kehli</i>	QM F7882	Warren & Hutchinson, 1983
<i>Keratobrachyops australis</i>	QM F10115, 10119, 14487, 14488	Warren, 1981; Damiani & Warren, 1996
<i>Pelorocephalus</i> spp.		Marsicano, 1993
Rhytidosteidae	UTGD 87784, QM F6471, 10121, 14490	Nilsson, 1946b; Cosgriff & Zawiske, 1979; Warren & Black, 1985
<i>Thoosuchus jakovlevi</i>	AM F98271	Getmanov, 1989
Trematosauridae	unregistered material at NMV, UCMP 112135 (c)	Jaekel, 1922; Mazin & Janvier, 1983; Hellrung, 1987
<i>Tersomius</i> spp.		Carroll, 1964; Daly, 1994
Trematopidae	AMNH 7150, MCZ 2475	Berman, Reisz & Eberth, 1987; Dilkes, 1990
<i>Dissorophus</i> spp.	MCZ, 1695	Carroll, 1964; DeMar, 1968
<i>Eryops</i> spp.	AMNH 43149, MCZ 1129, 1840, 7765, 1793, 2648, 1219, 1220, 12 2587, 7783.	Sawin, 1941; Moulton, 1974
Zatrachydidae	UCMP 34158(c), MCZ 2169, 2738, 2744	Langston, 1953; Boy, 1989

* Note the UCMP material, here referred to *Batrachosuchus*, is a collection of disarticulated elements (including good postcranial material) from a single locality in the Orange Free State that may or may not belong to this genus but definitely pertains to a derived brachyopid.

Rhinesuchidae, the monophyly of which has not been well supported and which Milner (1990b) regards as paraphyletic. Since data on the morphology of rhinesuchids is scarce, postcranial characters from *Uranocentrodon* were combined with cranial characters from *Rhineceps* in this analysis. Since all rhinesuchids have a similar morphology, they are at worst a close knit paraphyletic 'grade' of organization on the stem of a larger clade. It therefore seems unlikely that the potential chimaera used here will have any effect on the overall topology found by the analysis. It does mean that any ghost lineage implied by the Rhinesuchidae is not necessarily as old as the oldest rhinesuchid. When the condition for a character was variable amongst the members of a family level terminal taxon the presumed ancestral condition was coded in the data matrix, provided a reasonable phylogeny of the family was available, otherwise the character was coded as an uncertainty. An undescribed genus and species of *Tupilakosaurus*-like temnospondyl from the Karoo of South Africa (Warren, submitted) was included because it is important for resolving the position of the bizarre and incompletely known *Tupilakosaurus*. *Saurerpeton obtusum* and *Isodectes megalops* are regarded as synonymous following the work of Sequeira & Milner (1996). Similarly *Blinasaurus henwoodi* is regarded as a species of *Batrachosuchus* following Warren & Marsicano (1998).

As the larvae of temnospondyls have a markedly different morphology compared to post-metamorphic individuals, the bulk of the characters pertain to the condition in mature, post-metamorphic individuals. Therefore any terminal taxa had to be represented by adult or subadult material at the very least. For this reason the families Branchiosauridae and Micromelerpetontidae were not included in the analysis. Branchiosaurids are known only from larval to metamorphic individuals (Schoch, 1992) and while the largest micromelerpetontids might be reproductive adults, they remain highly paedomorphic (Daly, 1994). Nevertheless ontogenetic characters are important and are used in this analysis. Those few taxa for which ontogenetic series are available then become especially valuable. In the case of *Eryops*, for which there is little ontogenetic data, the states of character 55 (the ontogenetic timing of suturing between the parasphenoid-pterygoid articulation) and 18 (the degree of flexure of the infraorbital sulcus, which happens to be absent in adult *Eryops* and its relatives) were taken from the ontogenetic series of *Onchiodon* (Boy, 1990), which is an undoubted close relative of *Eryops* (Boy, 1990; Milner, 1990a, b). Similarly the character 55 in *Lydekkerina* was taken from a partial ontogenetic series of its relative, *Chomatobatrachus* (personal observation of UTGD material). Post-metamorphic specimens (probably subadults) of *Lapillopsis* are now available and allowed this taxon to be included in the analysis. A full description of this material will be published elsewhere (Yates, submitted).

The taxon-character matrix was analysed using the PAUP 3.1.1 cladistics package (Swofford, 1993). Due to the size of the matrix, the heuristic search algorithm was used with the following settings. The random addition sequence was used with 10 replicates. The tree bisection-reconnection branch swapping algorithm was used.

Bremer support values for each node were obtained by searching for the most parsimonious tree not compatible with a constraint tree. The constraint tree contains only the node being tested, all others being collapsed into polytomies. This yields the difference between the most parsimonious tree containing the particular clade being tested, and the most parsimonious tree without it. The difference is thus a measure of strength of that clade (Bremer, 1988). As a method of comparing our results with those of previous hypotheses the shortest trees that conformed to

alternative contents of the Stereospondylomorpha tax. nov. (the Stereospondyli + Archegosauroidae) were searched for. This was achieved by enforcing constraint trees that differed from the most parsimonious tree but were consistent with the alternative hypothesis. Three such constraint trees were used. The first kept most of the Stereospondylomorpha tax. nov. together but excluded the Brachyopidae in accordance with the hypotheses of Milner (1990b) and Shishkin (1973) which derive the Brachyopidae from the Dvinosauroidae, which are unrelated to the Stereospondyli. The second is very similar except that the Chigutisauridae is also excluded in accordance with the hypothesis of Damiani & Warren (1996). The third tree has a less diverse Stereospondyli that includes only long snouted forms as implied by Shishkin, Rubidge & Kitching (1996).

ABBREVIATIONS

Institutional abbreviations

AM	Australian Museum, Sydney
ALM	Albany Museum, Grahamstown
AMNH	American Museum of Natural History, New York City
BMNH	Natural History Museum, London
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MGUH	Museum Geologicum Universitatis Hafniensis, Copenhagen
MNHN	Musée National d'Histoire Naturelle, Paris
NMV	Museum of Victoria, Melbourne
PIN	Paleontological Institute, Moscow
QM	Queensland Museum, Brisbane
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UCMP	University of California Museum of Paleontology, Berkeley
UCMZ	University of Cambridge Museum of Zoology, Cambridge
USNM	National Museum of Natural History, Washington
UTGD	University of Tasmania Geology Department, Hobart
WAM	Western Australian Museum, Perth

Anatomical abbreviations

a	angular	pqf	paraquadrate foramen
eo	exoccipital	ps	parasphenoid
f	frontal	pt	pterygoid
g	glenoid socket	ptf	post-temporal fenestra
mx	maxilla	sa	surangular
q	quadrate	sol	supra-orbital lamina
qj	quadratojugal	sq	squamosal
os	oral sulcus	st	supratemporal
pal	palatine	t	tabular
pmx	premaxilla	v	vomer

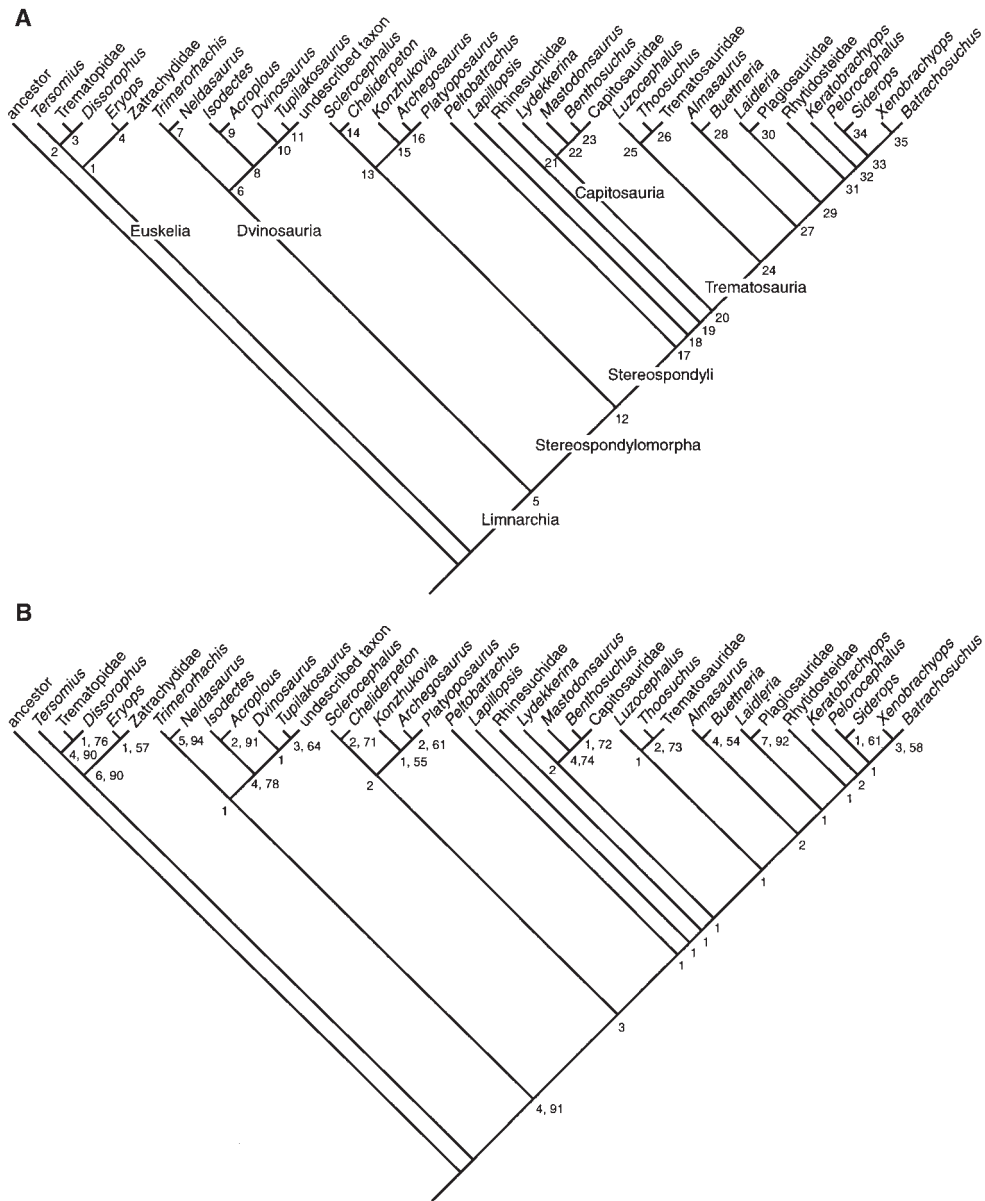


Figure 1. A, most parsimonious tree found by this analysis. Tree length = 452 steps; consistency index = 0.325; retention index = 0.669. Numbers refer to clade numbers in the text. B, most parsimonious tree with Bremer support values (left number) for each clade and bootstrap frequencies (right number) for each clade compatible with the 50% majority rule consensus tree of the bootstrap analysis.

RESULTS

A single most parsimonious tree of 452 steps, with a consistency index of 0.325 and a retention index of 0.669 (Fig. 1) was recovered. The character state changes

supporting each clade are given below. The number that precedes each character refers to the number of the character in appendix 1. The character state changes were optimized using delayed transformation (DELTRAN).

Character state changes that shift from one node to another under different optimisation regimes are listed as ‘ambiguous synapomorphies’ while those that are tied to one node despite differing the optimisation are listed as ‘unambiguous synapomorphies’, following the terminology of Holtz (1994) and Chiappe, Norell & Clark (1996). The terms ‘ambiguous’ and ‘unambiguous’ are not meant to imply the presence or absence of homoplasy in the distribution of that character state. This means that an unambiguous synapomorphy may be reversed deeper into the clade or appear convergently in another clade. Ambiguity may be caused by missing data or incongruence in the data. Those character state changes that are free from homoplasy (Consistency Index=1.00) are marked with an asterisk (*). The phylogenetic taxonomic system (de Queiroz & Gauthier, 1992) is used. Since no temnospondyl taxa have been formally defined in the phylogenetic sense, definitions are given with each named clade, including those that have been previously named.

Clade 1

Euskelia tax. nov. (Fig. 2)

Etymology. Greek, *eu*=well or true, *skelos*=limb, in reference to the well ossified limb bones with well developed crests and processes for muscle attachments that typify this group.

Phylogenetic definition. A stem-based taxon including all temnospondyls that share a more recent common ancestor with *Eryops* than with *Parotosuchus*.

Included taxa. *Eryops*, Zatrachydidae, *Tersomius*, Trematopidae and *Dissorophus*.

Unambiguous synapomorphies. (11) Width of the postparietals exceeds four times the length (Fig. 2); (13)* large plate-like septomaxilla situated on the floor of the nasal cavity, with limited contact with the skull roof; (15) length of the posterior skull table shortened so that it is less than 46% of the width; (19)* descending squamosal flange lying immediately in front, and parallel to, the antero-lateral surface of the ascending ramus of the pterygoid; (52) loss of dorsal process of the palatine; (54) elongate cylindrical to hemicylindrical internal process of the pterygoid abutting the basal process of the parasphenoid (Fig. 2); (55)* suturing of the pterygoid-parasphenoid articulation late in post-metamorphic ontogeny; (93) posterior meckelian foramen shifted anteriorly so that it is bordered exclusively by the postsplenial and the prearticular; (116)* large ventrally placed radial capitellum on the humerus (Fig. 2).

Ambiguous synapomorphies. (1) Intertemporal bone absent so that the postfrontal and supratemporal suture; (34) basioccipital reduced so that the occipital condyle is bilobed; (114) supinator process of the humerus separate from the deltopectoral crest (Fig. 2).

Remarks. The descending squamosal flange has been described and figured by Bolt (1974c, fig. 3) and Dilkes (1993, fig. 2) for trematopids, and by Carroll (1964, fig. 4B) for *Tersomius*. It is also present in *Eryops* (personal observation of MCZ 1129). Its presence or absence could not be determined in *Dissorophus* or Zatrachydidae.

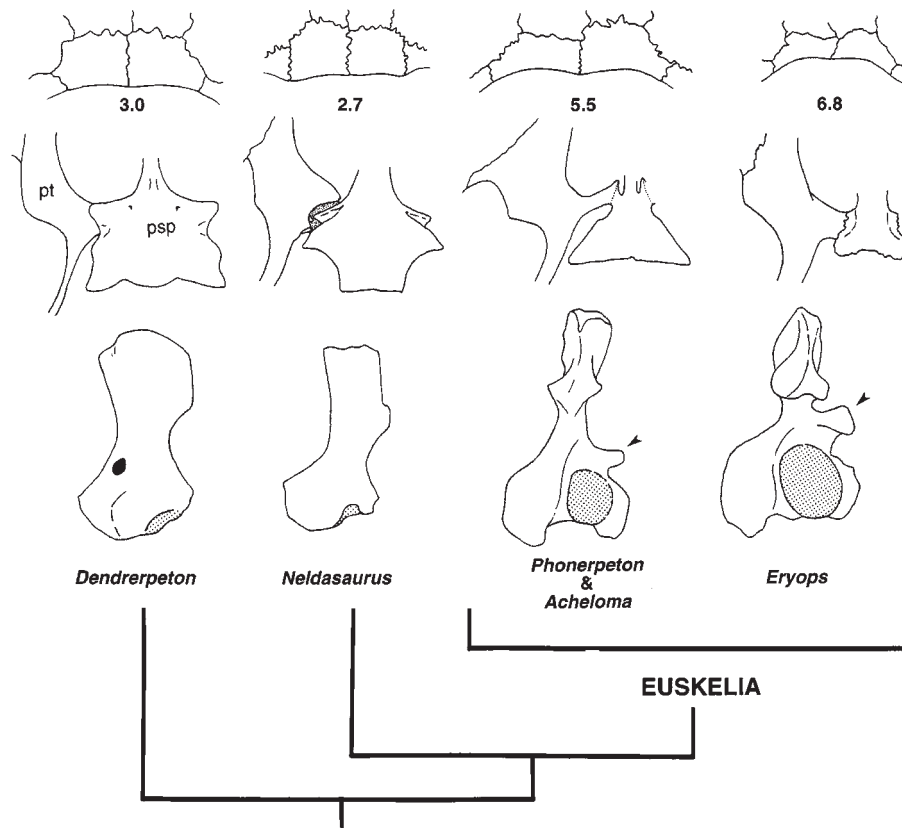


Figure 2. Phylogenetic diagram showing the postparietals in dorsal view and the width:length ratio of the pair (top row), right pterygoid-parasphenoid articulation in ventral view (middle row) and humerus in ventral view (bottom row) in Euskelia and successive outgroups. The apomorphic conditions of Euskelia are: antero-posteriorly short postparietals (width:length ratio >4) (character 11); an elongate, cylindrical to hemicylindrical internal process of the pterygoid, abutting the parasphenoid (character 54); a well developed and discrete supinator process of the humerus (arrowed) (character 114); and a large ventrally facing convex facet for the articulation of the radius (stippled) (character 116). Figures redrawn from the following sources: *Dendrerpeton helogenes* (postparietals and palate – Milner, 1996); *Dendrerpeton acadianum* (humerus – Carroll, 1967); *Neldasaurus wrightae* (Chase, 1965); the trematopids *Phonerpeton pricei* (postparietal – Dilkes, 1990) and *Acheloma cummingsi* (palate and humerus – Olson, 1941); and *Eryops megacephalus* (postparietals and palate—Sawin, 1941, humerus – Gregory, 1949).

Clade 2

Dissorophoidea (Williston, 1910)

Phylogenetic definition. A stem-based taxon including all Euskelians that share a more recent common ancestor with *Dissorophus* than with *Eryops*.

Included taxa. *Tersomius*, Trematopidae, *Dissorophus*.

Unambiguous synapomorphies. (2) Exposure of the dorso-lateral margin of the palatine in the orbital margin; (4) frontals contributing to the orbital margins; (9) ventral flange of the prefrontal inside the orbital margin; (10)* ventral flange of the nasal; (41)* dorsal process on the quadrate; (42)* medial process on the quadratojugal;

(105) height of neural spines less than or equal to the length between the pre- and postzygapophyses.

Remarks. As the focus of this analysis was on the origins and relationships of Mesozoic temnospondyls, relatively few dissorophoids were included. As a result it is possible that some of the synapomorphies found to diagnose the Dissorophoidea in this analysis may be an artifact of the small number of taxa analysed. As an example, several dissorophoids are known to have a prefrontal-postfrontal contact excluding the frontals from the orbit. Thus it may be that the frontal contribution to the orbital margin diagnoses a less inclusive clade than the Dissorophoidea, or possibly has evolved on more than one occasion within the clade.

Clade 3

Unnamed taxon

Included taxa. Trematopidae and *Dissorophus*.

Unambiguous synapomorphies. (38) Loss of stapedial foramen; (120) dorsal osteoderms enlarged to form ornamented armour plates.

Clade 4

Eryopoidea (Cope, 1882)

Phylogenetic definition. A stem-based taxon including all Euskelians that share a more recent common ancestor with *Eryops* than with *Dissorophus*.

Included taxa. *Eryops* and Zatrachydidae.

Unambiguous synapomorphy. (6) Jugal extends anteriorly to orbit.

Ambiguous synapomorphies. (25) Orbits behind the mid length of the skull; (117) vertical iliac blade.

Remarks. Eryopoidea has traditionally included a range of long snouted, moderately derived, Palaeozoic temnospondyls including eryopids, zatrachydids, actinodontids and archegosaurids. Our analysis finds that this assemblage is polyphyletic, therefore the Eryopoidea is redefined in a much narrower sense than it has been used in the past.

Clade 5

Limnarchia tax. nov. (Fig. 3)

Etymology. Greek, *limne* = marsh or lake, *archon* = ruler, refers to both the success of this diverse and long lived clade and the aquatic adaptations displayed by most of its members.

Phylogenetic definition. A stem-based taxon including all temnospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Eryops*.

Included taxa. *Neldasaurus*, *Trimerorhachis*, *Dvinosaurus*, *Tupilakosaurus*, undescribed genus, *Acroplous*, *Isodectes*, *Konzhukovia*, *Sclerocephalus*, *Cheliderpeton*, *Platyoposaurus*, *Archegosaurus*, *Peltobatrachus*, *Lapillopsis*, Rhinesuchidae, *Lydekkerina*, Capitosauridae, *Mastodonsaurus*,

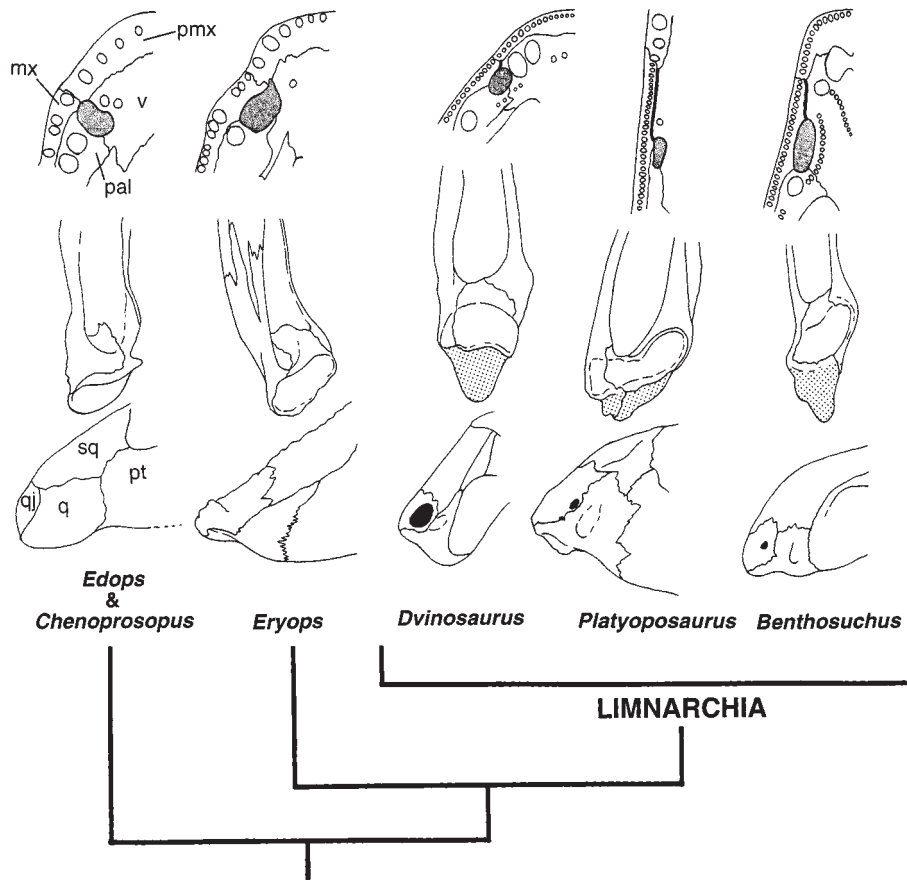


Figure 3. Phylogenetic diagram showing right anterior palate in ventral view (top row), posterior left mandible in dorsal view (middle row) and left quadrate area in occipital view (bottom row) in Limnarchia and successive outgroups. The apomorphic conditions of Limnarchia are: a maxilla-vomer suture (heavy line) (character 64); a post-glenoid area on the mandible (stippled) (character 89); and a paraquadrate foramen (character 43). Shaded areas in the top row represent the choanae. Figures redrawn from the following sources: the edopoids *Edops craigi* (palate and mandible) (Romer & Witter, 1942) and *Chenoprosopus lewisi* (quadrate area) (Hook, 1993); *Eryops megacephalus* (Sawin, 1941); *Dvinosaurus primus* (Shishkin, 1973); *Platyoposaurus stuckenbergi* (Gubin, 1991); and *Benthosuchus sushkini* (Bystrow & Efremov, 1940).

Benthosuchus, *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteidae, *Laidleria*, Plagiosauridae, *Almasaurus*, *Buettneria*, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops* and *Batrachosuchus*.

Unambiguous synapomorphies. (43) A paraquadrate foramen on the occipital face of the quadratojugal (Fig. 3); (50) a perforated anterior palatal fossa; (59) an ectopterygoid tooththrow; (61) pterygoid with a conical recess dorsal to the pterygoid-parasphenoid articulation; (64) maxilla suturing with the vomer (Fig. 3); (77) loss of denticles on the vomers; (89)* post-glenoid area on the mandible (Fig. 3); (109)* interclavicle elongated, so that it is at least 1.3 times as long as broad.

Remarks. Bjerring (1997) thought that the conical recess of the pterygoid was restricted to Triassic forms with an elongated pterygoid-parasphenoid suture, but it is also

clearly present in *Neldasaurus* (Chase, 1965) and *Trimerorhachis* (observation of AMNH material), which have a plesiomorphic parasphenoid-pterygoid articulation. Furthermore, we believe that the depression in the pterygoid of *Dvinosaurus* that was described as the ‘fossa articularis’ by Shishkin (1973) is homologous with the conical recess of other limnarchians. Both depressions occur in the same position, immediately anterior to the medial end of the ascending ramus of the pterygoid.

Clade 6

Dvinosauria tax. nov.

Phylogenetic definition. A stem-based taxon including all limnarchians that share a more recent common ancestor with *Dvinosaurus* than with *Parotosuchus*.

Included taxa. *Trimerorhachis*, *Neldasaurus*, *Dvinosaurus*, *Tupilakosaurus*, undescribed genus, *Acroplous*, *Isodectes*.

Unambiguous synapomorphies. (17) Sensory sulci present on the skull roof of adults; (28) reduction of the otic notch to a shallow embayment; (56) loss of postero-lateral flange on palatine ramus of the pterygoid; (107)* 28 or more presacral vertebrae.

Ambiguous synapomorphy. (71) loss of denticles on the parasphenoid; (74) paired anterior palatal fossae.

Remarks. In the past this assemblage has been referred to as the Trimerorhachoidea. This name is not applied here for the following reason. The name Dvinosauroidae is available for the more exclusive clade of *Dvinosaurus* + (Eobrachyopidae + Tupilakosauridae) which is a well supported clade and deserves a name. Although the concept of rank is downplayed in phylogenetic systematics it is still undesirable to have a taxon that is of traditional superfamily rank, i.e. the Dvinosauroidae, nested within another superfamily, i.e. the Trimerorhachoidea. The solution here is to erect a new suprafamilial taxon, the Dvinosauria, for the total group and restrict the name Trimerorhachoidea to all dvinosaurians more closely related to *Trimerorhachis* than to *Dvinosaurus*. At the moment the use of Trimerorhachoidea is redundant, for it only contains Trimerorhachidae, but non-trimerorhachid trimerorhachoids can be expected to be discovered in the future. Indeed the poorly known *Eugyrinus* may be just such an animal.

Clade 7

Trimerorhachidae Cope, 1891

Phylogenetic definition. A node-based taxon including *Trimerorhachis*, *Neldasaurus* and all descendants of their most recent common ancestor.

Included taxa. *Trimerorhachis* and *Neldasaurus*.

Unambiguous synapomorphies. (15) Posterior skull table elongated so that the length is at least 90% of the width; (78) more than eight palatine teeth; (80) a posteriorly broadening sulcus behind the pterygoid process of the parasphenoid; (84) an elongate posterolateral process of the vomer extends along the medial edge of the palatine, posterior to the palatine tusks; (92) reversal so that the posterior coronoid is hidden when the mandible is in lateral view; (97) mandibular sulcus deeply incised at its

posterior end; (117) a vertical iliac blade; (118) iliac blade antero-posteriorly flared at its dorsal end.

Ambiguous synapomorphies. (18) A step-like flexure in the infraorbital sulcus between the orbit and the naris; (30) squamosal and tabular suturing on the skull roof; (67) Muscular crests surrounding ‘pockets’ on the ventral surface of the parasphenoid.

Clade 8

Dvinosauroida Säve-Söderbergh, 1935

Phylogenetic definition. A node-based taxon including all descendants of the common ancestor of *Dvinosaurus* and *Isodectes*.

Included taxa. *Dvinosaurus*, *Tupilakosaurus*, undescribed genus, *Isodectes*, *Acroplous*.

Unambiguous synapomorphies. (5) Loss of the posteriorly projecting triangular process of the premaxilla, medial to the naris; (11) antero-posteriorly shortened postparietals; (23)* tabulars reduced to thin silvers on the posterior margin of the supratemporal; (28) otic notch lost; (48) the posterior face of the quadrate ramus of the pterygoid is twisted to face ventrally and is strongly downturned creating a vaulted palate; (52) dorsal process of palatine is exposed on the dorsal skull roof; (75) an almost straight medial margin of the subtemporal fossa; (87) loss of pterygoid denticulation; (99)* post glenoid area of mandible with a transverse trough behind the glenoid followed by a dorsally bulging tip (Fig. 4).

Ambiguous synapomorphies. (25) Orbits in front of midline; (83) alar process of the jugal posterior to the ectopterygoid.

Remarks. There is conflicting character evidence regarding the internal relationships of this clade. At only one step away from the most parsimonious tree an alternative arrangement where the Eobrachyopidae and Tupilakosauridae are sister-groups, is found. Characters that support this grouping include: palatine contribution to the interpterygoid vacuity, palatine and vomer contact lateral to the choana and clavicle facets on interclavicle contacting anteriorly. It is important to note that the character states for *Dvinosaurus* are taken strictly from *D. primus*, the type species of the genus. ‘*Dvinosaurus*’ *egregius* differs from *D. primus* in several of the characters used in this analysis. It probably occupies a different phylogenetic position to *D. primus*, though it is almost certainly a dvinosauroid.

Clade 9

Eobrachyopidae (= Saurerpetontidae Chase, 1965) Shishkin, 1964

Phylogenetic definition. A stem-based taxon including all dvinosauroids that share a more recent common ancestor with *Isodectes* than with either *Dvinosaurus* or *Tupilakosaurus*.

Included taxa. *Isodectes* and *Acroplous*

Unambiguous synapomorphies. (17) Sensory sulci of skull roof restricted to a single circumorbital sulcus in adults; (27) prefrontal contributes to the narial margin; (59) reversal to the absence of an ectopterygoid tooththrow; (72)* parasphenoid plate transversely expanded, creating lateral wings.

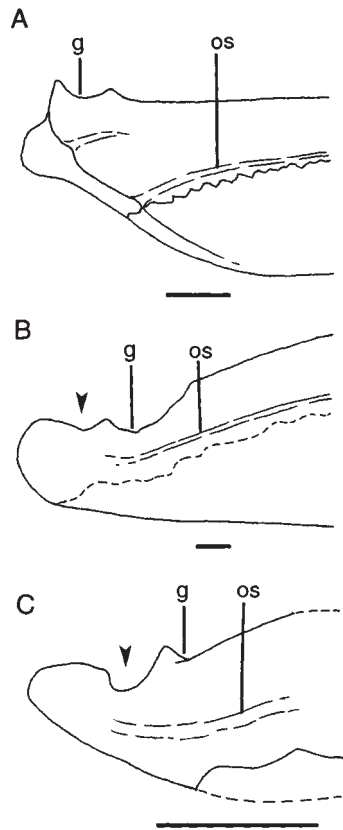


Figure 4. The posterior end of the lower jaw in lateral view of various temnospondyls displaying the states for character 99. A, *Trimerorhachis insignis* (from Nilsson, 1944). B, *Dvinosaurus primus* (from Shishkin, 1973). C, *Tupilakosaurus wethugensis* (from Shishkin, 1973). B and C show the derived condition of a transverse trough (arrowed) behind the glenoid followed by a dorsally bulging tip. Scale bars = 10 mm.

Ambiguous synapomorphies. (51) Palatine ramus of the pterygoid does not extend anterior to the palatine tusks; (60) antero-posterior constriction of the vomers so that there is only a narrow bar between the anterior end of the cultriform process and the anterior palatal fossa; (73) midline keel on the ventral surface of the cultriform process; (76) vomer and palatine suturing lateral to the choana, thus excluding the maxilla from the choanal margin.

Clade 10

Unnamed taxon

Included taxa. *Dvinosaurus*, *Tupilakosaurus*, undescribed genus.

Unambiguous synapomorphies. (1) Intertemporal absent with a postorbital-parietal suture; (3) lacrymals absent; (63) a transverse toothrow on the vomers, between the vomerine tusks; (101) a single toothrow on all three coronoids.

Ambiguous synapomorphies. (18) Infraorbital sulcus with a step-like flexure between the orbit and the naris; (36) presence of a palatoquadrate fissure; (57) width of the

cultriform process at its narrowest point more than 10% of the length of the interpterygoid vacuities; (121) ossified ceratobranchials in adults.

Clade 11

Tupilakosauridae Kuhn, 1960

Phylogenetic definition. A stem-based taxon including all dvinosauroids sharing a more recent common ancestor with *Tupilakosaurus* than with either *Isodectes* or *Dvinosaurus*.

Included taxa. *Tupilakosaurus* and an undescribed genus from South Africa.

Unambiguous synapomorphies. (37) Ascending column on the posterior face of ascending ramus of the pterygoid; (44) tabular and exoccipital contacting in the paroccipital process; (54) corpus of the pterygoid forming a broad contact along the lateral margins of the parasphenoid plate; (103) intervening pleurocentra preventing adjacent intercentra from contacting along their ventral edge; (104) intercentra closed dorsally over the notochord.

Ambiguous synapomorphies. (30) Squamosal-tabular suture; (51) palatine ramus of the pterygoid does not extend anterior to the palatine tusks; (76) vomer and palatine suturing lateral to the choana, thus excluding the maxilla from the choanal margin.

Clade 12

Stereospondylomorpha tax. nov.

Phylogenetic definition. A node-based taxon including *Archegosaurus* and *Parotosuchus* and all descendants of their common ancestor.

Included taxa. *Konzhukovia*, *Cheliderpeton*, *Sclerocephalus*, *Platyoposaurus*, *Archegosaurus*, *Peltobatrachus*, *Lapillopsis*, Rhinesuchidae, *Lydekkerina*, Capitosauridae, *Mastodonsaurus*, *Benthosuchus*, *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteiidae, *Buettneria*, *Almasaurus*, *Laidleria*, Plagiosauridae, *Pelorocephalus*, *Keratobrachyops*, *Siderops*, *Xenobrachyops* and *Batrachosuchus*.

Unambiguous synapomorphies. (6) Jugal extends anterior to the orbit; (7) prefrontal-jugal suture; (12) maxilla-nasal suture; (90) arcadian groove on the post glenoid area of the mandible.

Ambiguous synapomorphies. (1) Loss of intertemporal with a postfrontal-supratemporal suture; (34) bilobed occipital condyle with reduced basioccipital contribution; (67) muscular crests surrounding ‘pockets’ on the ventral surface of the parasphenoid; (83) alar process of the jugal posterior to the ectopterygoid.

Clade 13

Archegosauroidea (Meyer, 1857)

Phylogenetic definition. A stem-based taxon including all stereospondylomorphs sharing a more recent common ancestor with *Archegosaurus* than with *Parotosuchus*.

Included taxa. *Cheliderpeton*, *Sclerocephalus*, *Konzhukovia*, *Archegosaurus* and *Platyoposaurus*.

Unambiguous synapomorphies. (24) Thin crest below tabular horn (usually extending posterior to ornamented dorsal surface); (68) posterior premaxillary teeth larger than

anterior premaxillary and maxillary teeth; (93) posterior meckelian foramen bordered by the postsplenial and prearticular alone.

Ambiguous synapomorphies. (25) Orbits placed behind midline of skull; (58) absence of ectopterygoid tusks; (74) paired anterior palatal fossae; (78) palatine tooththrow of at least four teeth.

Remarks. Unlike Milner (1990b) and Gubin (1997) we find that these taxa form a clade rather than a paraphyletic grade on the stem of the Stereospondyli. All but one of the characters previously used to support the hypothesis that archegosauroids share a more recent common ancestor with stereospondyls than with actinodontids are associated with skull elongation, a very common and plastic feature in temnospondyl evolution. The one character not associated with skull elongation is the presence of a thin ventral crest on the tabular (Gubin, 1997). The distribution of this character, however, does not support the hypothesis for not only is it probably present in the actinodontid, *Sclerocephalus* (indeterminate in *Cheliderpeton*) it is absent in the Stereospondyli, outside of the Rhinesuchidae. We interpret the occurrence of the character in both the Archegosauroidae and the Rhinesuchidae as an example of convergence. This interpretation is backed by the lack of any such ridge in the well preserved tabular horns of the basal stereospondyls, *Peltobatrachus* and *Lapillopsis*.

Clade 14

Actinodontidae Lydekker, 1885

Phylogenetic definition. A stem-based taxon including *Sclerocephalus* (= *Actinodon*) and all archegosauroids sharing a more recent common ancestor with it than with *Archegosaurus*.

Included taxa. *Sclerocephalus* and *Cheliderpeton*.

Unambiguous synapomorphies. (17) Sensory sulci on the skull roof of adults; (50) reversal to imperforate anterior palatal fossae; (64) reversal to maxilla and vomer not in contact; (80) a short sulcus becoming wider and deeper postero-laterally, behind the pterygoid articulation.

Ambiguous synapomorphy. (71) Parasphenoid denticles forming a transverse belt between the pterygoid-parasphenoid articulations.

Clade 15

Archegosauridae Meyer, 1857

Phylogenetic definition. A stem-based taxon including *Archegosaurus*, and all archegosauroids that share a more recent common ancestor with it than with *Sclerocephalus*.

Included taxa. *Konzhukovia*, *Archegosaurus* and *Platyoposaurus*.

Unambiguous synapomorphies. (5) Absence of a triangular process of the premaxilla projecting posteriorly, medial to the naris; (88)* a rugose, medial, premaxillary tubercle between the anterior palatal fossae.

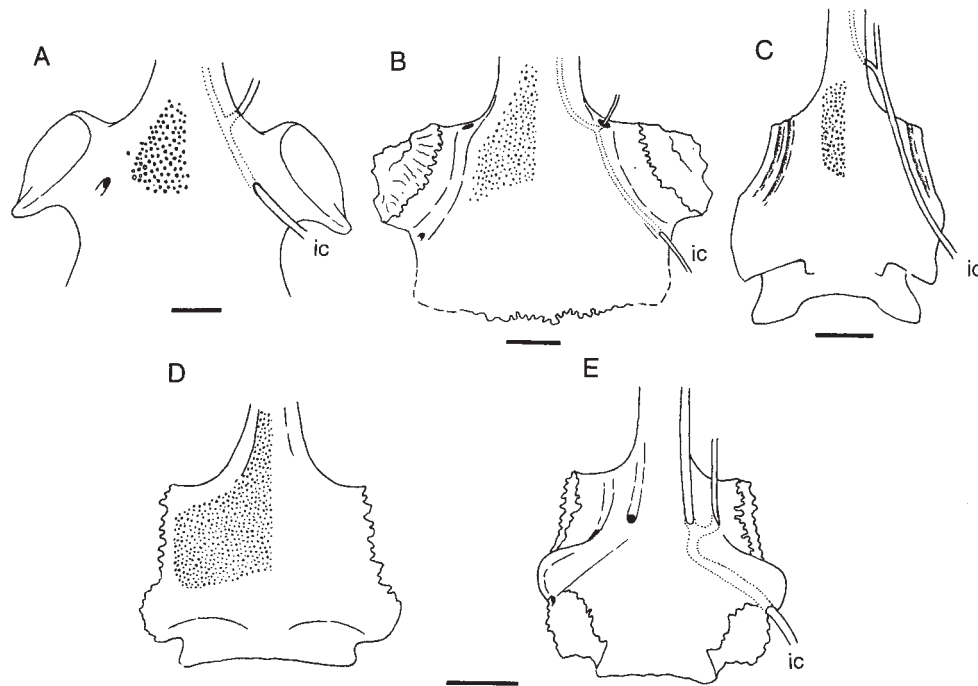


Figure 5. A–D, ventral view of temnospondyl parasphenoids showing arterial pathways and the states for character 62. A, *Edops craigi* (drawn from MCZ 1235). B, *Eryops* sp. (drawn from AMNH 43149). C, *Platyoposaurus stuckenbergi* (from Shishkin, 1968). D, *Benthosuchus sushkini* (from Bystrow & Efremov, 1940). E, *Benthosuchus sushkini* parasphenoid in dorsal view. Only the denticles on the left side are shown, dotted lines indicate where the arteries pass through bone. (A) shows the plesiomorphic condition where the internal carotid enters the parasphenoid through the ventral surface of the plate, medial to the pterygoid-parasphenoid articulation. (B) shows derived state 1 where the internal carotid enters through the lateral surface of the parasphenoid plate, posterior to the pterygoid-parasphenoid articulation. (C) shows derived state 3 where the internal carotid passes through a groove on the ventral surface of the parasphenoid plate. (D, E) show derived state 2 where the internal carotid enters the parasphenoid plate from the dorsal surface. Scale bars = 10 mm.

Clade 16

Unnamed taxon.

Included taxa. *Archegosaurus* and *Platyoposaurus*.

Unambiguous synapomorphies. (21) Lateral margins of snout parallel or concave; (77) reversal to denticulate vomers; (78) eight or more palatine teeth.

Ambiguous synapomorphy. (62) Internal carotid artery passing along the ventral surface of the parasphenoid plate, leaving a groove, with a foramen on the lateral side of the parasphenoid at the base of the cultriform process (Fig. 5).

Clade 17

Stereospondyli Fraas, 1889

Phylogenetic definition. A stem-based taxon including all stereospondylomorphs that share a more recent common ancestor with *Parotosuchus* than with *Archegosaurus*.

Included taxa. *Peltobatrachus*, *Lapillopsis*, Rhinesuchidae, *Lydekkerina*, Capitosauridae, *Benthosuchus*, *Mastodonsaurus*, *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteidae, *Almasaurus*, *Buettneria*, *Laidleria*, Plagiosauridae, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (51) Palatine ramus of pterygoid retracted posteriorly so that the palatine is exposed in the interpterygoid vacuity; (54) pterygoid with a flat, broad internal process articulating with most of the lateral edge of the parasphenoid plate; (86) ventral surface of pterygoids bear ornament.

Ambiguous synapomorphies. (62) Internal carotids passing through the dorsal surface of the parasphenoid (either on the surface or just below it) (Fig. 5); (71) parasphenoid denticle field forms a transverse 'belt' between the pterygoid-parasphenoid articulations; (119) intercondylar fossa at the distal end of the femur reduced to a small weak depression.

Remarks. The ontogenetic character state of an early suturing of the parasphenoid and pterygoid appears to be a significant character that separates stereospondyls from all other temnospondyls. These bones are sutured in extremely small, immediately post-metamorphic, or possibly late larval individuals of the basal stereospondyl *Lapillopsis nana* (Warren & Hutchinson, 1990a), the capitosaurid *Parotosuchus aliciae* (Warren & Hutchinson, 1988), and an unnamed rhytidosteid (cf. *Arcadia myriadens* in Warren & Hutchinson, 1990b). Post-metamorphic juvenile individuals are known for lydekkerinids (Cosgriff, 1974), *Benthosuchus* (Bystrow & Efremov, 1940), *Thoosuchus* (Getmanov, 1981), and metoposaurids (Hunt, 1993), all of which have sutured pterygoid-parasphenoid articulations. In contrast in the stereospondyl outgroups the pterygoid-parasphenoid articulation sutures only once adult size has been reached such as in the eryopid *Onchiodon* (Boy, 1990), or remain unsutured throughout life. This character state cannot be determined in *Peltobatrachus* which is only known from adult material. Nevertheless the articulation is sutured in these adults, so the plesiomorphic condition of remaining unsutured throughout life is clearly not present. Thus, although the actual node at which this character state change occurs remains ambiguous, it seems quite likely that it diagnoses the whole of the Stereospondyli as it is understood in this analysis.

Clade 18

Unnamed taxon.

Included taxa. *Lapillopsis*, Rhinesuchidae, *Lydekkerina*, *Benthosuchus*, *Mastodonsaurus*, Capitosauridae, *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteidae, *Almasaurus*, *Buettneria*, *Laidleria*, Plagiosauridae, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (15) Length of posterior skull table less than 65% of its width; (40) an oblique ridge on the posterior face of the quadrate ramus of the pterygoid; (44) tabular-exoccipital suture in the paroccipital process; (102) large hamate process on the mandible.

Ambiguous synapomorphy. (55)* Pterygoid-parasphenoid articulation suturing at (or about) metamorphosis.

Clade 19

Unnamed taxon

Included taxa. Rhinesuchidae, *Lydekkerina*, *Benthosuchus*, *Mastodonsaurus*, Capitosauridae, *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteidae, *Almasaurus*, *Buettneria*, *Laidleria*, Plagiosauridae, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (5) Absence of a triangular process of the premaxilla projecting posteriorly medial to the naris; (8) maxilla and quadratojugal only making point contact or not contacting at all; (17) sensory sulci on the skull roof of adults; (56) loss of posterolateral flange on the palatine ramus of the pterygoid; (63) transverse vomerine tooththrow; (79) vomerine tooththrow along medial border of choana.

Ambiguous synapomorphies. (58) Ectopterygoid tusks absent in adults; (78) more than eight teeth in palatine tooththrow.

Clade 20

Unnamed taxon

Included taxa. *Lydekkerina*, *Benthosuchus*, *Mastodonsaurus*, Capitosauridae, *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteidae, *Almasaurus*, *Buettneria*, *Laidleria*, Plagiosauridae, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (34) Double occipital condyles with no contribution to the articular surface from the basioccipital; (95) denticle field lost from all three coronoids; (101) tooththrow on posterior coronoid.

Ambiguous synapomorphies. (16) Supraorbital laminae narrowly spaced either side of the midline on the ventral surface of the frontals (Fig. 6); (26) tabular horns extend posterior to the level of the postero-lateral corners of the skull; (30) squamosal-tabular suture on the skull roof; (37) ascending column on the posterior face of the ascending ramus of the pterygoid; (53) palatine ramus of the pterygoid retracted posterior to the first ectopterygoid tooth; (91) prearticular does not extend anterior to the level of the suture of the middle and posterior coronoids; (105) height of dorsal neural spines less than the distance between the pre- and postzygapophyses; (110) clavicular facets on interclavicle in contact anteriorly; (112) anteriorly projecting flange with a thickened central rib on the anterior edge of the dorsal process of the clavicle (Fig. 7); (115) ectepicondyle of the humerus is a low rounded bump.

Remarks. The large number of ambiguous characters diagnosing this clade is the result of missing data for Rhinesuchidae. Thus these characters could diagnose this clade or the previous one (clade 19).

Clade 21

Capitosauria tax. nov.

Phylogenetic definition. A stem-based taxon including all stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Siderops*.

Included taxa. *Lydekkerina*, *Benthosuchus*, *Mastodonsaurus*, Capitosauridae (including *Parotosuchus*).

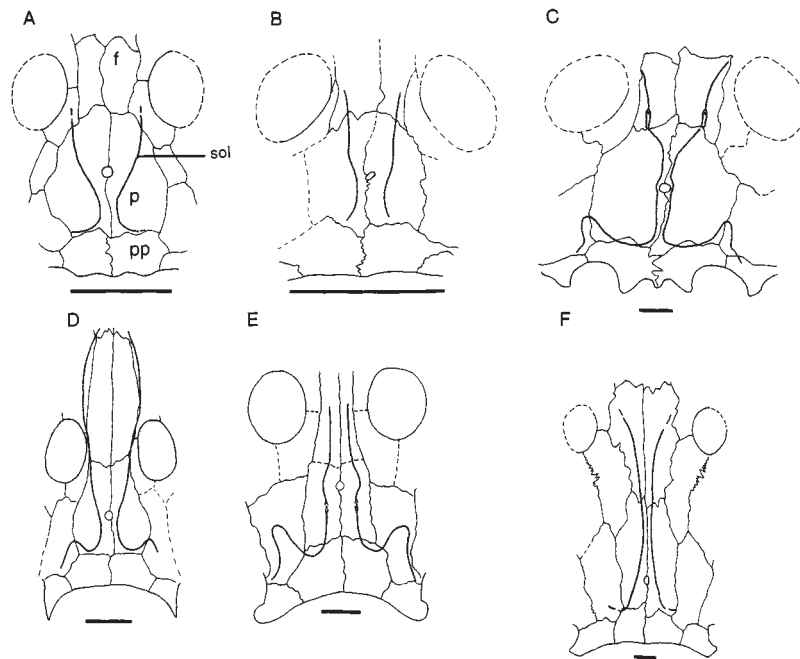


Figure 6. Ventral view of skull roof showing the relationship of the system of ridges (supraorbital laminae) to the frontals in various temnospondyls and the states for character 16. A, the basal temnospondyl *Denderpeton acadianum* (from Shishkin, 1973). B, the trematopid *Phonerpeton pricei* (from Dilkes, 1990). C, *Dvinosaurus primus* (from Shishkin, 1973). D, *Archegosaurus decheni* (from Gubin, 1997). E, *Konzhuskovia vetusta* (from Gubin, 1991). F, the metoposaurid *Metoposaurus diagnosticus* (from Shishkin, 1973). (A–D) show the plesiomorphic condition of having the supra-orbital laminae broadly flared on the frontals. (E, F) show the derived condition of narrowly spaced supra-orbital laminae on the frontals. Scale bars = 20 mm.

Unambiguous synapomorphies. (18) Presence of a step like flexure in the infra-orbital sulcus; (69) elongate posterior process of palatine extending posterior to ectopterygoid tusks.

Ambiguous synapomorphies. (14) Squamosal margin of the otic notch is convex in dorsal view; (29) terminal crest on the ventral surface of the tabular horn.

Remarks. The analysis found that above a few basal stem forms, the Stereospondyli is divisible into two clades, one containing *Parotosuchus* and its close relatives, the other containing the Trematosauridae and a variety of families including some short faced forms. Much the same arrangement was found by Warren & Black (1985) in the first cladistic study of Mesozoic temnospondyls. Most workers (e.g. Milner, 1990a, b) nevertheless regard the Trematosauridae as derived members of the capitosauroid radiation. The genera *Benthosuchus* and *Thoosuchus* have been proposed as intermediates bridging the Trematosauridae to typical capitosauroids (Getmanov, 1986, 1989). Based on our analysis we regard the similarity between *Benthosuchus* and *Thoosuchus* as a result of their relative plesiomorphic nature and thus resemblance to the common ancestor of Capitosauria tax. nov. and Trematosauria tax. nov.

The name Capitosauroides was established as a suborder by Säve-Söderbergh (1935), however it is not used here as it is too easily confused with the more exclusive

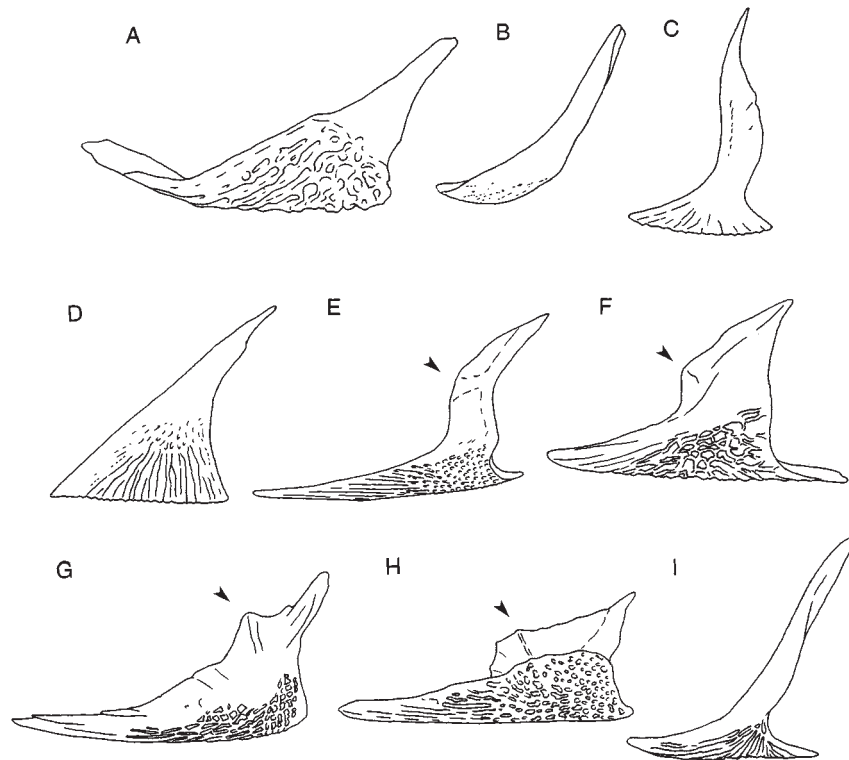


Figure 7. Left clavicles of various temnospondyls in lateral view showing the states for character 112. A, colosteid *Greerpeton burkemorani* (from Godfrey, 1989). B, *Eryops* sp. (drawn from MCZ 7765). C, *Dvinosaurus primus* (from Shishkin, 1973). D, *Sclerocephalus haeuseri* (from Meckert, 1993). E, *Benthosuchus sushkini* (from Bystrow & Efremov, 1940). F, capitosaurid *Paracyclotus davidi* (from Watson, 1958). G, trematosaurid *Lyrocephaliscus euri* (from Mazin & Janvier, 1983). H, *Buettneria perfecta* (from Sawin, 1945). I, *Siderops kehli* (from Warren & Hutchinson, 1983). E–H have the derived condition of an anterior flange (prescapular process) on the dorsal process with a thickened central rib (arrowed).

and more widely used taxon, Capitosauroida (Watson, 1919). Warren & Black (1985) used the term “capitosaurian” for this group but did not formally name the taxon. Therefore the taxon is named the Capitosauria here.

Clade 22

Unnamed taxon (‘capitosauroids’)

Included taxa. *Benthosuchus*, *Mastodonsaurus*, Capitosauridae.

Unambiguous synapomorphies. (14) Squamosal margin of the otic notch has an overhanging falciform crest; (18) flexure on the infra-orbital sulcus ‘z’ shaped; (40) sharp edged crest-like oblique ridge on the posterior face of the quadrate ramus of the pterygoid; (67) muscular crests not strongly curved and approaching each other at the midline of the parasphenoid plate; (78) more than eight palatine teeth.

Remarks. This clade contains the taxa traditionally placed in the Capitosauroida (Watson, 1919). However, this family group name does not have priority. A detailed review of this clade by Damiani (in prep.) will deal with its taxonomy.

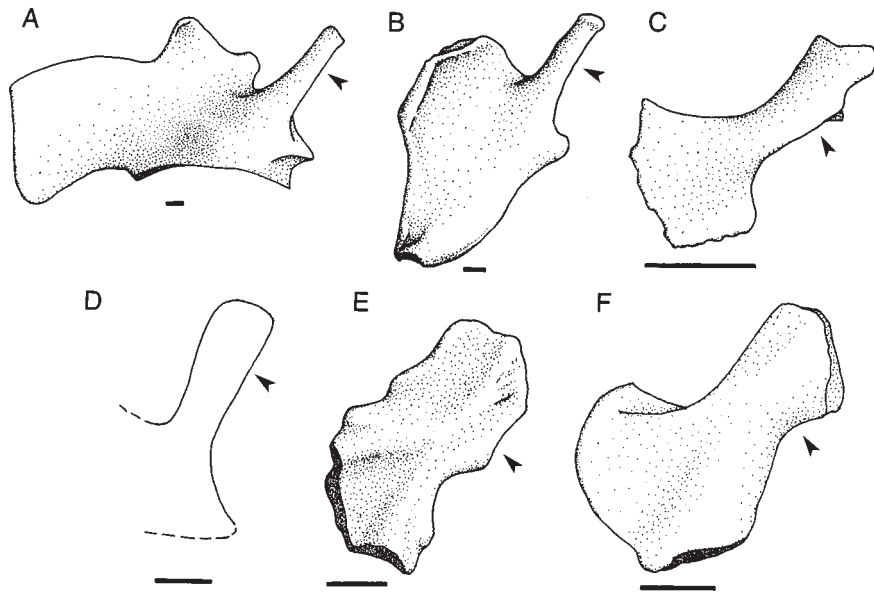


Figure 8. The left epipterygoid of various temnospondyls in anterior view showing the states for character 85. A, edopoid *Edops craigi* (from Romer & Witter, 1942). B, *Eryops megacephalus* (from Sawin, 1941). C, trematosaurid, *Lyrocephalus euri* (from Mazin & Janvier, 1983). D, unidentified rhytidosteid from the Arcadia Formation (drawn from QM F14490, the epipterygoid is only visible in posterior view in this specimen hence only the medial outline of the bone can be seen). E, *Benthosuchus sushkini* (from Bystrow & Efremov, 1940). F, capitosaurid *Parotosuchus gunganj* (drawn from QM F10114). (E, F) show the derived condition of a robust ascending process. Scale bars = 5 mm.

Clade 23

Unnamed taxon

Included taxa. Capitosauridae and *Benthosuchus*.

Unambiguous synapomorphies. (95) Denticle patches absent from all three coronoids; (111) supraglenoid buttress not co-ossified with the coracoid plate, transforming the supraglenoid foramen to a ventrally open notch; (118) iliac blade anteroposteriorly flared at its dorsal end.

Ambiguous synapomorphies. (81) Dorsal surface of the parasphenoid plate with parapterygoid crests (*sensu* Bystrow & Efremov, 1940); (85)* robust ascending ramus of the epipterygoid (Fig. 8).

Clade 24

Trematosauria tax. nov.

Phylogenetic definition. A stem-based taxon including all stereospondyls that share a more recent common ancestor with *Trematosaurus* than with *Parotosuchus*.

Included taxa. *Thoosuchus*, Trematosauridae, *Luzocephalus*, Rhytidosteidae, *Almasaurus*, *Buettneria*, *Laidleria*, Plagiosauridae, *Siderops*, *Keratobrachyops*, *Pelorocephalus*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (33) Interorbital space greater than 50% of the skull width at the mid orbital level; (38) loss of stapedial foramen; (67) reversal to the absence of sharp rimmed depressions at the posterior end of the ventral surface of the parasphenoid plate; (95) denticle patches absent from all three coronoids; (100) chorda tympanic foramen located on the prearticular; (102) reversal to the absence of a hamate process.

Remarks. This taxon was first named the Trematosauroidae by Sæve-Söderbergh (1935) and later referred to as the ‘trematosaurian’ group by Warren & Black (1985).

Clade 25

Unnamed taxon

Included taxa. *Luzocephalus*, *Thoosuchus* and Trematosauridae.

Unambiguous synapomorphies. (15) reversal to the length of the posterior skull table being between 70% and 90% of its width; (36) ascending ramus of the pterygoid does not contact the squamosal, creating a palatoquadrate fissure.

Clade 26

Trematosauroidae (Watson, 1919)

Phylogenetic definition. A node based taxon including *Thoosuchus* and *Trematosaurus* and all descendants of their common ancestor.

Included taxa. *Thoosuchus* and Trematosauridae.

Unambiguous synapomorphies. (39)* Parasphenoid plate extending posteriorly to cover the pedicels of the exoccipital condyles in ventral view; (66) cultriform process laterally compressed so that the sides meet to form a midline ventral keel; (74) paired anterior palatal fossae.

Ambiguous synapomorphies. (29) Terminal crest on the ventral surface of the tabular horn; (81) parapterygoid crests on the dorsal surface of the parasphenoid plate.

Clade 27

Unnamed taxon

Included taxa. *Almasaurus*, *Buettneria*, *Laidleria*, Plagiosauridae, Rhytidosteidae, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (40) Reversal to the absence of an oblique ridge on the posterior face of the quadrate ramus of the pterygoid; (71) parasphenoid denticles absent; (82) contribution from the ectopterygoid to the strut separating the interpterygoid vacuity from the subtemporal fossa.

Ambiguous synapomorphies. (25) Orbits located in front of the midline of the skull; (90) reversal to the absence of an arcadian groove at the posterior end of the mandible.

Clade 28

Metoposauroidae (Watson, 1919)

Phylogenetic definition. A node based taxon including *Almasaurus* and *Metoposaurus* and all descendants of their common ancestor.

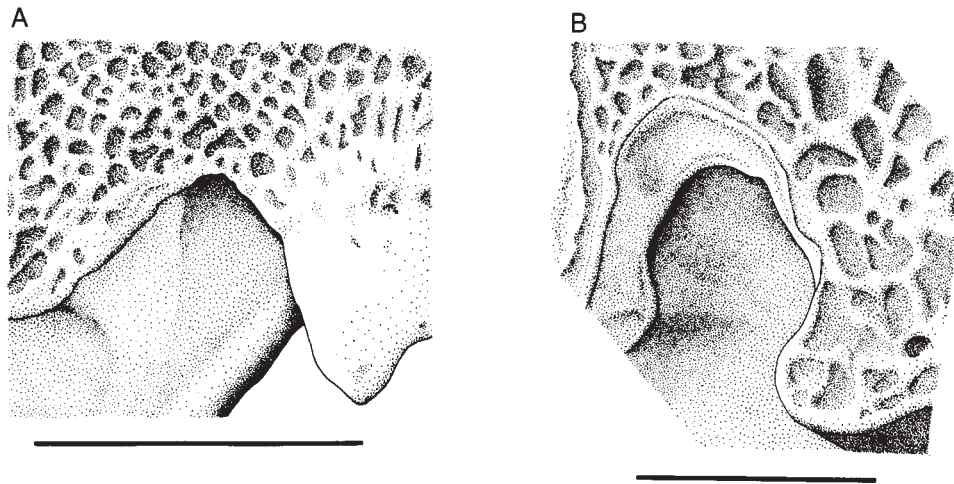


Figure 9. The right otic notch of A, *Lydekkerina huxleyi* (UCMZ T221) and B, *Almasaurus habbazi* (MNHN ALM43) in dorsal view, displaying the states for character 22. *Almasaurus* shows the derived condition of a sharp edged 'gutter' bordering the otic notch. Scale bars = 10 mm.

Included taxa. *Almasaurus* and *Buettneria* (a close relative of *Metoposaurus*).

Unambiguous synapomorphies. (15) Length of posterior skull table greater than 90% of its width; (18) infra-orbital sulcus with a step-like flexure between the orbit and the naris; (22)* 'gutter' bordered by ridges around the margin of the otic notch (Fig. 9); (70) exoccipital-pterygoid suture visible in ventral view; (74) paired anterior palatal fossae; (113)* keeled lateral margin of the clavicle.

Ambiguous synapomorphy. (87) Pterygoid denticles absent.

Clade 29

Unnamed taxon

Included taxa. *Laidleria*, Plagiosauridae, Rhytidosteidae, *Keratobrachyops*, *Siderops*, *Pelorocephalus*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (14) Reversal to a straight or concave posterior margin of the squamosal; (28) otic notch reduced to a wide shallow embayment; (111) supraglenoid buttress of the scapulocoracoid not co-ossified with the coracoid plate, changing the supraglenoid foramen to a ventrally open notch; (114) reversal to the absence of a discrete supinator process on the humerus.

Ambiguous synapomorphies. (48) Quadrate ramus of the pterygoid untwisted so that it forms a near horizontal plate, continuous with the plane of the corpus and palatine ramus of the same bone; (76) posterolateral process from the vomer approaching an anterolateral process of the palatine on the lateral margin of the choana, thus reducing the maxillary contribution to the choanal margin.

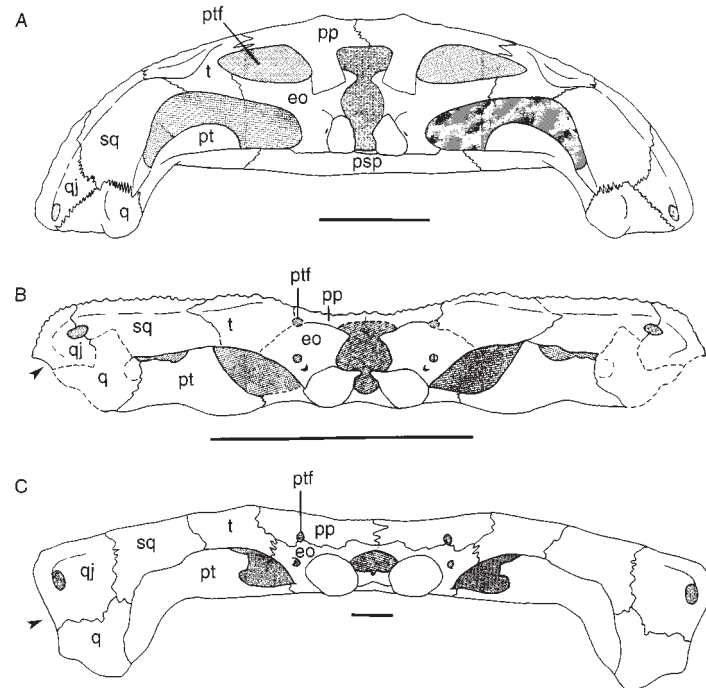


Figure 10. Skulls of Plagiosauroida and a related outgroup in occipital view. A, *Arcadia myriadens* (from Warren & Black, 1985). B, *Laidleria gracilis* (modified from Warren, 1998). C, the plagiosaurid *Plagiosternum danilovi* (from Shishkin, 1987). Apomorphic conditions of the plagiosauroids (*Laidleria* and *Plagiosternum*) are highly reduced posttemporal fenestrae (character 46) and an overhanging quadratojugal separated from the quadrate by a sulcus (arrowed) (character 35). Scale bars = 30 mm.

Clade 30

Plagiosauroida (Abel, 1919) (Fig. 10)

Phylogenetic definition. A node based taxon including *Laidleria* and *Plagiosaurus* and all descendants of their most recent common ancestor.

Included taxa. *Laidleria* and Plagiosauridae.

Unambiguous synapomorphies. (4) Frontals contribute to the orbital margins; (6) reversal to jugal not extending anteriorly to the orbit; (28) otic notch absent; (33) reversal to narrowly spaced orbits; (35)* sulcus between the lateral margin of the quadrate condyle and the postero-lateral corner of the quadratojugal, visible in occipital view (Fig. 10); (46)* reduction of the posttemporal fenestrae to small foramina or absent altogether (Fig. 10); (106)* neural spines with lateral buttresses; (108) pleurocentra highly reduced or absent; (120) tessellating mosaic of ornamented, dorsal osteoderms.

Ambiguous synapomorphies. (87) Pterygoid denticles absent; (105) height of neural spines of mid dorsal vertebrae less than 40% of the distance between pre and postzygapophyses.

Remarks. This grouping is rather unconventional as *Laidleria* is usually thought to be a rhytidosteid or rhytidosteid relative (e.g. Milner, 1990b; Warren, 1998). However, *Laidleria* does not share any apomorphic characters with the Rhytidosteidae that

would indicate a close relationship, beyond the straight sided triangular shape of the skull. Notably absent are such rhytidosteid characters as an extensive denticle field covering the whole palate; transversely short, triangular shaped quadrate condyles; broad cultriform process and denticles lateral to the dentary tooththrow. Apart from its relatively long, pointed snout, *Laidleria* is quite similar to the Plagiosauridae. The intercentra of *Laidleria* are more elongate than is usual in temnospondyls and seem to be approaching the dorsally closed, spool-like condition seen in plagiosaurids. Whether the intercentra of *Laidleria* close dorsally, as they do in plagiosaurids, cannot be determined at present.

Clade 31

Unnamed taxon

Included taxa. Rhytidosteidae, *Siderops*, *Pelorocephalus*, *Keratobrachyops*, *Xenobrachyops*, *Batrachosuchus*.

Unambiguous synapomorphies. (3) Lachrymals absent; (58) reversal to the presence of enlarged ectopterygoid tusks at the anterior end of the ectopterygoid; (95) reversal to the presence of a patch of denticles on the posterior coronoid; (101) reversal to the absence of a row of teeth on any of the coronoids.

Clade 32

Brachyopoidea (Lydekker, 1885)

Phylogenetic definition. A node based taxon containing *Keratobrachyops* and *Brachyops* and all descendants of their most recent common ancestor.

Included taxa. *Keratobrachyops*, *Siderops*, *Pelorocephalus*, *Xenobrachyops* and *Batrachosuchus*.

Unambiguous synapomorphies. (18) Infraorbital sulcus with a step-like flexure between the orbit and the naris; (47)* posteriorly curved ascending ramus of the pterygoid; (48) quadrate rami of pterygoids strongly downturned creating a vaulted palate; (112) reversal to the absence of an anterior flange on the dorsal process of the clavicle.

Remarks. *Keratobrachyops* has been referred to the Chigutisauridae in the past (Warren, 1981; Damiani & Warren, 1996). However we find there is weak support for the genus occupying a position basal to the Brachyopidae–Chigutisauridae dichotomy. In this light the clavicle (QM F10122) found close to the holotype of *Keratobrachyops australis* is interesting. A small weakly expressed anterior flange is present on the dorsal process whereas this process is absent in other brachyopoid clavicles. If QM F10122 does belong to the holotype of *Keratobrachyops* (as seems likely) then the reduction of the anterior flange would diagnose the Brachyopoidea, while its complete loss would diagnose a less inclusive clade, the Chigutisauridae + Brachyopidae.

Clade 33

Unnamed taxon

Included taxa. *Siderops*, *Pelorocephalus*, *Xenobrachyops* and *Batrachosuchus*.

Unambiguous synapomorphies. (70) Exoccipital-pterygoid suture visible in ventral view; (86) reversal to the absence of ornament on the ventral surface of the pterygoids;

(96) prearticular extending posterior to the glenoid, covering the medial face of the articular.

Clade 34

Chigutisauridae Rusconi 1951

Phylogenetic definition. A stem-based taxon including all brachyopoids sharing a more recent common ancestor with *Pelorocephalus* (= *Chigutisaurus*) than with *Brachyops*.

Included taxa. *Siderops* and *Pelorocephalus*.

Unambiguous synapomorphies. (45)* Medial end of ascending ramus of the pterygoid is strongly curved posteriorly in horizontal section; (93) posterior meckelian foramen bordered by the prearticular and postsplenial exclusively.

Ambiguous synapomorphies. (49) Substapedial ridge on the pterygoid; (75) straight lateral edge of the pterygoid bordering the subtemporal vacuity.

Clade 35

Brachyopidae Lydekker, 1885

Phylogenetic definition. A stem-based taxon including all brachyopoids sharing a more recent common ancestor with *Brachyops* than with *Pelorocephalus*.

Included taxa. *Xenobrachyops* and *Batrachosuchus* (a close relative of *Brachyops*).

Unambiguous synapomorphies. (6) Reversal to jugal not extending anteriorly to the orbit; (28) otic notch absent; (78) reversal to the absence of a toothrow behind the palatine tusks; (79) reversal to the absence of a vomerine toothrow along the medial margin of the choana; (100) chorda tympanic foramen absent.

Ambiguous synapomorphy. (87) Pterygoid denticles absent.

DISCUSSION

Although there is much agreement between this analysis and that of Milner, (1990b), they differ in the topology of the basal nodes. Milner placed the eryopoid-dissorophoid clade (here called Euskelia) as the sister-group to the Stereospondyli and its stem (here called the Stereospondylomorpha) with the 'Trimerorhachoidea' (here called the Dvinosauria) outside this clade. In our analysis there is strong support for the grouping of the Dvinosauria with the Stereospondylomorpha in the taxon, Limnarchia. Limnarchia and Euskelia appear to represent two temnospondyl radiations into aquatic and terrestrial ecosystems, respectively. Most members of the Euskelia have been thought to be terrestrial as adults, while most members of the Limnarchia have been thought to be at least semi-aquatic (e.g. Romer, 1947; Carroll, 1988). Evidence for the terrestrial nature of euskelians comes from the well ossified nature of the articular ends of the limb bones, the well developed nature of the processes and scars for muscle attachment on those bones, the tall neural spines and well ossified vertebral elements of most members of this clade. The reduction of the dermal components of the pectoral girdle in euskelians may also be associated

with terrestrial locomotion. Evidence for the aquatic to semiaquatic nature of limnarchians comes from the well developed sensory sulci of the lateral line system on the skull roof and mandible of most members of the clade, and the generally poorly ossified condition of their limb bones. Some members, like plagiosaurids, *Trimerorhachis*, *Dvinosaurus* and tupilakosaurids were perennibranchiate (Nilsson, 1946a; Bystrow, 1938; Olson, 1979; Warren, submitted) confirming an aquatic lifestyle for at least these taxa.

Of course with diverse and long ranging clades, exceptions to these generalisations did evolve. *Peltobatrachus* is firmly nested within the Limnarchia yet it lacks sensory sulci on the skull roof and has well ossified limb bones with well developed muscle attachments indicating a terrestrial existence (Panchen, 1959). On the other hand, micromelerpetontids were probably aquatic dissorophoid euskelians (Boy, 1995; Daly, 1994).

The content of the Stereospondyli as defined in this analysis is very close to that of Romer's (1947) concept of the Stereospondyli, the major difference being that Romer excluded the Trematosauroida from his Stereospondyli. Many workers have rejected the monophyly of this assemblage, expressing the opinion that the characters that unite them are part of a 'Mesozoic grade of organization' that was acquired independently in all the separate lineages crossing the Permo-Triassic boundary. This hypothesis seems improbable and is not supported by our analysis.

It should be noted that the Bremer support values for most of the nodes within the Limnarchia, including the Stereospondyli, are one, the minimum possible support. This is partly due to the influence of poorly known taxa that have an unstable position within the cladogram, e.g. *Luzocephalus* and *Peltobatrachus*. If the taxa that cannot be coded for more than 30% of the characters (*Tupilakosaurus*, *Cheliderpeton*, *Konzhukovia*, *Peltobatrachus*, *Luzocephalus*, *Laidleria*, and *Batrachosuchus*) are excluded from the analysis the resulting six trees show a topology that is largely similar to the tree generated by the complete analysis. However, the Stereospondyli still has a Bremer support value of one. This is caused by the marked similarity of the Dvinosauroida and the Brachyopidae. In the analysis with deleted taxa it takes only one step to shift the Dvinosauroida from its basal position and place it deep within the Stereospondyli as the sister-group of *Xenobrachyops*. This is an unlikely arrangement, not least because it implies the existence of 12 ghost lineages extending back to the Carboniferous (nine of which do not have fossil records until the Mesozoic). Most past hypotheses (e.g. Watson, 1956; Shishkin, 1973; Coldiron, 1978; Foreman, 1990; Damiani & Warren, 1996) have regarded the Dvinosauroida as a paraphyletic group with respect to the Brachyopidae (or the Brachyopidae + Chigutisauridae in the case of Damiani & Warren, 1996) outside the Stereospondyli. The shortest tree in which the Stereospondyli does not include the Brachyopidae or the Dvinosauroida as hypothesized by Milner, (1990b) is six steps longer than the most parsimonious tree (Fig. 11). The shortest tree that conforms to the hypothesis of Damiani & Warren, (1996), where the chigutisaurids were also excluded from the Stereospondyli, is nine steps longer than the most parsimonious tree (Fig. 11). The shortest tree in which only the long snouted Mesozoic forms such as the capitosauroids and trematosauroids form a clade with the Permian archegosauroids is also nine steps longer than the most parsimonious tree (Fig. 11). From this we conclude that the concept of a monophyletic Stereospondyli including capitosauroids, trematosauroids and the various short faced Mesozoic taxa is well supported despite its low Bremer support. Many of the shared derived characters of dvinosauroids

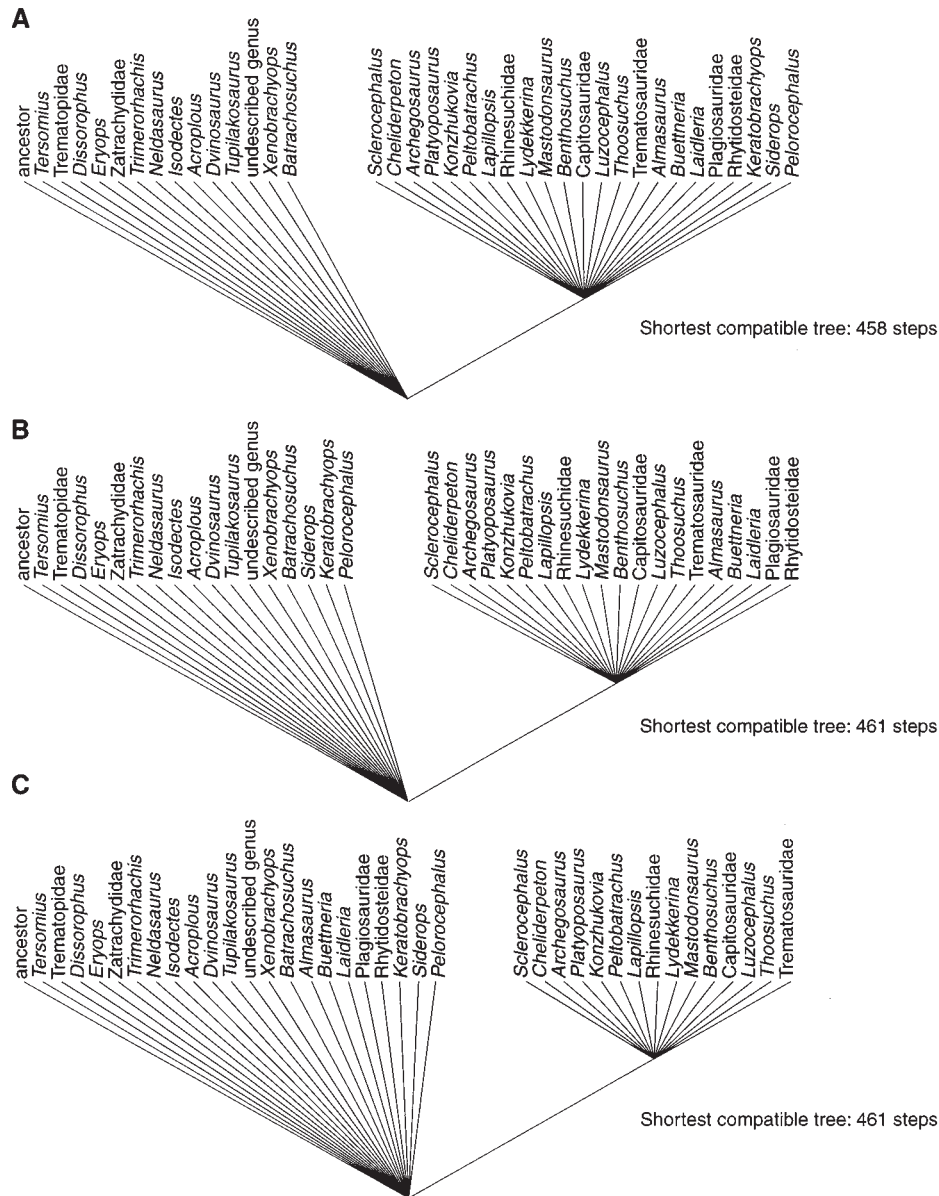


Figure 11. Constraint trees for various compositions of the Stereospondylomorpha n. tax. and the number of steps required to get a topology compatible with them. A, Brachyopidae is removed from the Stereospondylomorpha. B, Brachyopoidea is removed from the Stereospondylomorpha. C, Stereospondylomorpha includes only Archegosauroidae, basal stereospondyls, Capitosauria and Trematosauroidae.

and brachyopids relate to their unusual pterygoid morphology which creates a deep, vaulted palate. Both groups also possess large post-glenoid areas on the mandible, particularly well developed coronoid eminences, and short, broad snouts. All these features are thought to be adaptations to aquatic ambush predation, using suction-



Figure 12. A phylogenetic tree based on the present analysis. Solid columns represent known time ranges, thin lines represent 'ghost lineages'. E = Early. M = Middle. L = Late. STE = Stephanian. WES = Westphalian. NAM = Namurian.

gulping as the method of prey capture. Thus these characters could well be the result of convergence caused by similar methods of prey capture in both groups.

It is immediately apparent that nearly all Mesozoic temnospondyls belong to the Stereospondyli (Fig. 12). The only exceptions are the dissorophoid *Micropholis* and

the dvinosauroid family Tupilakosauridae. Both are restricted to the Early Triassic. Conversely, stereospondyls are rare in the Palaeozoic, where they are only known with certainty from the Permian of Gondwana. They are represented by the African basal forms *Peltobatrachus* and the family Rhinesuchidae and putative rhinesuchids from India (Werneburg & Schneider, 1996). There is also a possible rhytidosteid, *Trucheosaurus*, from the uppermost Permian of Australia (Marsicano & Warren, 1998). *Tryphosuchus* may be an exception to this observation. It is known from fragmentary material that does not necessarily belong to one taxon, from the Late Permian of Russia (Gubin, 1991). A few characters such as sensory sulci on the lower jaw, ornamented pterygoids and a single anterior palatal vacuity (if correctly restored), suggest that it may be more closely related to later stereospondyls than to the contemporary archegosaurids. If this were true the pathway of the internal carotid arteries, and the narrowness of the pterygoid-parasphenoid articulation would suggest that it is the plesiomorphic sister-group to all other stereospondyls. Like so many other taxa we eagerly await more complete remains of *Tryphosuchus*.

A number of scenarios could potentially explain these observations. First, it is possible that only a single species of stereospondyl survived the end Permian extinction event and it then proceeded to radiate spectacularly in the Early Triassic, filling the vacant niches left after the event. Second, the Stereospondyli could have been competitively superior to the other clades of temnospondyl present at the time, and directly caused their extinction by competitive exclusion. Third, the Stereospondyli may have been present as a component of many temnospondyl faunas in the Permian and some aspect of their biology fortuitously enabled them to survive the extraordinary environmental conditions that precipitated the Late Permian extinction event. Lastly, the Stereospondyli may have begun their radiation in the Permian but were restricted to a geographical area that was less severely affected by the end Permian extinction event than elsewhere in the world.

The first scenario would be falsified if the Late Permian *Trucheosaurus* could be confidently identified as a rhytidosteid. This would imply that much of the Stereospondyl radiation had already occurred before the end Permian event. Unfortunately the specimen is poorly preserved and few details can be ascertained. Nevertheless it is felt that the first scenario is the least likely because a wide range of derived stereospondyls, including capitosaurids, trematosaurids, rhytidosteids, plagiosaurids, chigutisaurids and brachyopids occur in the basal Triassic Arcadia Formation. This formation was correlated with the Nammalian Stage in a review of the Australian Triassic by Balme and Foster (1996, fig. 1), however there is little evidence to support this correlation. In a review of the age of the Arcadia Formation, Northwood (1997) found that a Griesbachian age was most likely for the vertebrate bearing horizons in the Arcadia Formation based on palynological data. This would leave little more than a million years for the Trematosauria, Capitosauria and most of the family level taxa within these clades to have diverged. It seems likely that the early evolution of the Capitosauria and Trematosauria began in the Late Permian.

The general paucity of Late Permian temnospondyl faunas makes it difficult to distinguish between the last three scenarios. The coincidence of the extinctions of most euskelians, dvinosaurians and archegosaurids with the greatest mass extinction event to have affected the biosphere, that of the Permo-Triassic boundary, renders the second scenario unlikely. Late Permian faunas in Eastern Europe include dissorophoids, archegosaurids and *Dvinosaurus* (Sennikov, 1996). Those in South America comprise archegosaurids (Barbarena, Aranjó & Lavina, 1985). India has

Late Permian archegosaurids, the probable stereospondylomorph *Lysipterygium*, and putative rhinesuchids (Werneberg & Schneider, 1996). It is only in the Permian of Africa that undoubted stereospondyls can be found. From these meagre data it would seem unlikely that stereospondyls were a major component of Late Permian temnospondyl faunas on any continent besides Africa or possibly Australia (of which the Late Permian fauna remains largely unknown). Thus the third scenario is implausible. Nevertheless a better record of temnospondyls across the Permian-Triassic boundary will be needed to confirm whether the temnospondyl extinctions really do coincide with the end Permian event. The fourth scenario is tentatively supported here. The geographical area, or 'safe haven' in which the stereospondyl radiation began would have been located in Gondwana. As mentioned earlier the only non-stereospondyl temnospondyls to have survived into the Mesozoic were *Micropholis* and the Tupilakosauridae. It is interesting to note that they are both found in South Africa, though tupilakosaurids had a wider distribution. Milner (1990b) similarly noted that the closest relatives of the Triassic temnospondyls appear to be Gondwanan, though some of the evidence he used is debatable. For example, neither is the Brachyopidae reliably recorded from the Permian of Australia (Warren & Marsicano, 1998), nor do we find an ancestor-descendant relationship between *Peltobatrachus* and Plagiosauridae likely.

The distribution of *Micropholis* and the Tupilakosauridae would appear to make Africa a likely location of the safe haven. Africa does have a reasonable Permian vertebrate record and basal stereospondyls are present. However the stereospondyl diversity is low, and all but *Peltobatrachus* are referable to one family, the Rhinesuchidae. Basal members of the Capitosauroidae, Trematosauroidae, Rhytidosteidae, Plagiosauroidae, Metoposauroidae and Brachyopoidea, which would be expected at the location of the initial stereospondyl radiation, are absent. At the time Africa was at the centre of a large land mass and was probably rather dry. This would account for the low temnospondyl diversity in the African Permian. Such a region is unlikely to host a major radiation of largely aquatic taxa. Perhaps the site of the stereospondyl radiation and the 'safe haven' was the then south coast of Antarctica. Australia is a less likely location, for no examples of surviving tupilakosaurids or dissorophoids have been found in the diverse Early Triassic faunas of this continent. We hope that, as the exploration of Antarctica continues, fossils to test our speculations will be discovered.

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APPENDIX 1

List of characters that vary within higher temnospondyls, used in our analysis. The list does not include characters that are autapomorphic for terminal taxa of our analysis. It was compiled from examination of original material (Table 1), descriptive literature and previous analyses. Literature used in the compilation of this list were: Bjerring, 1997; Bolt 1969; Bolt 1974a; Bolt, 1974b; Boy, 1990; Bystrow & Efremov, 1940; Chase, 1965; Daly, 1994; Damiani & Warren, 1996; Foreman, 1990; Gubin, 1997; Jupp & Warren, 1986; Milner, 1990b; Milner & Sequeira, 1994; Shishkin, 1968, 1987; Warren & Black, 1985; Warren & Hutchinson, 1983.

Cranial characters

- (1) Intertemporal present (0), absent with the resultant space occupied by a postfrontal-supratemporal suture (1), absent with a postorbital-parietal suture (2). As the two states represent two alternative configurations after the intertemporal has been removed the character is unordered.
- (2) Ventrolateral border of the orbit formed by the jugal and lachrymal (0), lateral edge of the corpus of the palatine exposed dorsally in the lateral margin of the orbit (1).
- (3) Lachrymals present (0), absent (1).
- (4) Pre- and post-frontals form a suture (0), pre- and post-frontals fail to contact so that the frontal contributes to the orbital margin (1).
- (5) Premaxilla with a triangular posterior process medial to the naris (0), triangular process absent, posterior dorsal margin of the premaxilla forming a simple suture with the nasal (1).
- (6) Anterior end of the jugal posterior to the anterior orbital margin (0), jugal extending beyond the anterior orbital margin (1).
- (7) Prefrontal and jugal not in contact (0), prefrontal and jugal form a suture (1).
- (8) Maxilla and quadratojugal form a suture (0), maxilla and quadratojugal only make point contact, or do not contact at all (1).
- (9) Prefrontal without a ventral process (0), prefrontal with a descending ventral flange on the orbital rim (1).
- (10) Nasal without a ventral flange (0) nasal with a ventral flange forming a posterior internal wall of the naris (1).
- (11) Postparietal pair less than 4 times wider, transversely, than anteroposteriorly long (0), greater than 4 times wider than long (1) (Fig. 2).
- (12) Maxilla and nasal not in contact (0), maxilla and nasal forming a suture (1).
- (13) Septomaxilla part of the skull roof forming the posterior nasal margin, or unossified (0), septomaxilla a large plate of bone forming the floor of the nasal cavity, with limited, if any, contact with the skull roof at the posterior nasal margin (1).
- (14) Straight or concave posterior squamosal margin in dorsal view (0), convex squamosal margin in dorsal view, bulging posteromedially narrowing the otic notch (1), convex and overhanging squamosal margin (falciform crest) (2). These character states form an ordered transformation series.
- (15) Length of the posterior skull table between 90% and 70% of its width (length measured as the sagittal distance from the level of the posterior edge of the orbits to the posterior margin of the skull

roof, width measured as the width from the lateral edge of one tabular to the other) (0), length of the posterior skull table 65–50% of the width (1), length of posterior skull table less than 46% of the width (2), length of posterior skull table greater than 90% of the width (3). These character states represent modifications away from the primitive state in different directions (shortening the skull table in states 1 & 2, lengthening it in state 3). For this reason the character is unordered.

(16) Supraorbital laminae on the ventral surface of the skull roof flared widely on the frontals (0), supraorbital laminae narrowly placed either side of the midline on the frontals (1) (Fig. 6).

(17) Sensory sulci absent from the skull roof of adults (0), extensive sensory sulci present on the skull of adults (1), sensory sulci of adults restricted to a single circumorbital sulcus (2). State 2, represents a further modification of state 1, therefore the character is treated as ordered.

(18) Infraorbital sulcus straight or gently curved (0), infra-orbital sulcus with a step-like flexure between the orbit and the naris (1), flexure 'Z' shaped (2). These character states form a clear transformation series so the character is ordered.

(19) Squamosal without a descending flange (0), squamosal with a descending flange lying immediately in front, and parallel to, the anterolateral surface of the ascending ramus of the pterygoid (1).

(20) Ornamentation of the dorsal skull roof consisting of ridges enclosing depressions, which become elongated in areas of skull elongation (0), ornamentation consisting of uniformly small pits enclosed by a network of ridges (1), ornament consisting of regularly spaced pustules (2). The two derived states are separate modifications of the primitive state, therefore the character is unordered.

(21) Snout margins continually converging towards tip (0), tip of snout expanded so that the snout margins run parallel, or are concave before the tip (1).

(22) Simple rounded or sharp edged posterodorsal margin of the skull roof around the otic notch (0), smooth 'gutter' bordered above and below by sharp ridges around the margin of the otic notch (1) (Fig. 9).

(23) Tabulars are well developed rectangular to triangular bones (0), tabulars reduced to thin slivers lying against the posterior margin of the skull roof (1).

(24) Tabular horn without a thin ventrally projecting crest of bone (0), tabular horn with a thin ventrally projecting crest of bone (frequently projecting posterior to the ornamented dorsal component of the horn) (1).

(25) Orbits located about half way along the skull length (0), orbits located in front of the midlength of the skull (1), orbits located behind midlength of the skull (2). The two derived states represent two alternative modifications of the plesiomorphic state that do not form a transformation series, therefore the character is left unordered.

(26) Tabular horns terminate anterior to the posterolateral corners of the skull roof (0), tabular horns extend posteriorly to the posterolateral corners of the skull roof (1).

(27) Prefrontal excluded from narial margin (0), prefrontal contributing to the narial margin (1).

(28) Otic notch deep (0), otic notch is a wide shallow embayment (1), otic notch absent (2). The character states represent successive stages in the reduction of the otic notch, therefore the character is treated as ordered.

(29) Tabular horn without a terminal crest (*sensu* Bystrow & Efremov, 1940) (0), terminal crest lying lateral and parallel to the buttress of the paroccipital process (= external tabular crest) (1).

(30) Squamosal and tabular separated by the supratemporal (0), squamosal-tabular suture present on the dorsal skull roof (1).

(31) Skull roof complete between the nostrils (0), medial internarial fenestra at the junction of the premaxillae and the nasals (1).

(32) Quadratojugal without a posterior spike (0) posteriorly projecting spike on the quadratojugal (1).

(33) Interorbital distance less than 50% of the width of the skull at mid orbital level (0), interorbital distance greater than 50% of the width of the skull at mid orbital level (1).

(34) Single occipital condyle with the basioccipital forming the largest contribution to the articulating surface (0), bilobed occipital condyle with reduced basioccipital contribution (1), double occipital condyles with no basioccipital contribution (2). Character state 1 represents an intermediate between state 0 and state 2, therefore the character is ordered.

(35) The quadratojugal forms a simple corner with the quadrate in occipital view (0), a sulcus present on the quadratojugal, lateral to the quadrate condyles, so that the quadratojugal forms an overhang in occipital view (1) (Fig. 10).

(36) Ascending ramus of the pterygoid contacts the squamosal (0), ascending ramus does not contact the squamosal, creating a palatoquadrate fissure (1).

- (37) Ascending ramus of the pterygoid without a thickened ascending column on its posterior surface (0), ascending column present (1).
- (38) Foramen passing through the stapes (0), stapedia foramen absent (1).
- (39) Pedicels of occipital condyles not covered by parasphenoid (0), pedicels covered in ventral view by a posterior extension of the parasphenoid plate (1).
- (40) Posterior face of quadrate ramus of the pterygoid without an oblique ridge (0) a low, rounded, oblique ridge present (1), oblique ridge is a large sharp edged crest (2). These character states form a clear transformation series and the character is ordered.
- (41) Occipital face of the quadrate without a dorsal process (0), quadrate with a dorsal process (1).
- (42) Quadratojugal without a medial process (0) posterior end of the quadratojugal with a medial process extending behind the quadrate condyle (1).
- (43) Occipital face of the quadratojugal without a foramen (0), paraquadrate foramen on the occipital face of the quadratojugal (1) (Fig. 3).
- (44) Tabular and exoccipital not in contact (0), tabular and exoccipital contacting in the paroccipital process (1).
- (45) Ascending ramus of the pterygoid gently concave posteriorly, in horizontal section (0), medial end of the ascending ramus strongly curved posteriorly in horizontal section (1).
- (46) Posttemporal fenestrae large (0), posttemporal fenestrae reduced to small foramina or entirely closed (1) (Fig. 10).
- (47) Ascending ramus of the pterygoid erect (0), dorsal end of ascending ramus posteriorly curved (1).
- (48) Quadrate ramus of the pterygoid twisted from the plane of the corpus and the palatine ramus, to form a subvertical plate (0), quadrate ramus untwisted, forming a near horizontal plate, continuous with the plane of the corpus and palatine ramus (1), quadrate ramus untwisted and strongly downturned, creating a vaulted palate (2). State 2 represents a further modification on top of an already untwisted quadrate ramus of the pterygoid, therefore the character is treated as ordered. The character will be discussed more fully elsewhere (Yates, in prep.).
- (49) Dorsal surface of the corpus of the pterygoid without a substapedial ridge (0), a substapedial ridge on the dorsal surface of the corpus of the pterygoid posterior to the ascending ramus (1).
- (50) Anterior palatal fossa not perforated (0), anterior palatal fossa perforated to form an anterior palatal vacuity (1).
- (51) Pterygoids extend anteriorly to the palatine tusks (0) pterygoids not extending anterior to the level of the palatine tusks (1).
- (52) A dorsal process of the palatine underplating the lachrymal (0), dorsal process absent (1), dorsal process present and exposed on the dorsal skull roof (2). This multistate character presents two alternative modifications of the dorsal process of the palatine, consequently it is unordered.
- (53) Palatine ramus of the pterygoid extends anterior to the anterior-most ectopterygoid tooth (0), palatine ramus retracted posterior to the first ectopterygoid tooth (1).
- (54) Parasphenoid articulates with depression in the corpus of the pterygoid, behind a short triangular medial process of the pterygoid (0) (Fig. 2), an elongate cylindrical to hemicylindrical medial process of the pterygoid abuts the parasphenoid (1) (Fig. 2), corpus of the pterygoid forming a broad contact along the lateral margins of the parasphenoid plate (2). A cylindrical medial process is not morphologically intermediate between the primitive state and a broad pterygoid-parasphenoid contact, thus the character is unordered.
- (55) Pterygoid-parasphenoid articulation remaining unsutured throughout life (0), pterygoid-parasphenoid articulation sutured late in post-metamorphic ontogeny (1), pterygoid-parasphenoid articulation sutured by the end of metamorphosis (2). This character could potentially represent a transformation series in which the timing of suturing is shifted to an earlier stage of ontogeny. However, it does not seem necessary to pass through state 1 to transform state 0 into state 2, therefore we have opted to leave this character as unordered.
- (56) Palatine ramus of the pterygoid bears a posterolateral flange (0), flange absent (1).
- (57) The width of the cultriform process of the parasphenoid at its mid point is less than 10% of the length of the process (using the anterior and posterior ends of the interpterygoid vacuities as the length of the cultriform process) (0), width of cultriform process more than 10% of its length (1).
- (58) Ectopterygoid with enlarged tusks at its anterior end (0) ectopterygoid tusks absent (1).
- (59) Ectopterygoid with only one or two teeth (0), ectopterygoid with a toothrow of more than three teeth (1).
- (60) Vomers form a large sheet of bone between the anterior end of the cultriform process and the

posterior edge of the anterior palatal fossa (0), vomers forming a narrow bar between the anterior end of the cultriform process and the posterior edge of the anterior palatal fossa (1).

(61) Pterygoid without a conical recess (0), a conical recess on the pterygoid above the pterygoid-parasphenoid articulation (1).

(62) Foramen for the internal carotid artery on the ventral surface of the parasphenoid plate, medial to the articulation with the pterygoid. Palatine artery branch exiting the parasphenoid on the lateral edge of the parasphenoid plate, anterior to the pterygoid articulation. Intracranial branch of the carotid remaining internal to the parasphenoid, extending up the cultriform process (0). Foramen for the internal carotid located on the lateral side of the parasphenoid plate, posterior to the pterygoid articulation (1). Internal carotid and the palatine and intracranial branches pass through the dorsal surface of the parasphenoid plate, either leaving foramina where they pass below the surface or grooves where they lie upon it (2). Internal carotid artery passing along the ventral surface of the parasphenoid plate, leaving a groove, with a foramen on the lateral side of the parasphenoid at the base of the cultriform process, where the intracranial branch enters the parasphenoid (3) (Fig. 5). These character states form several alternative arrangements that cannot be placed in a clear transformation series hence the character is unordered.

(63) Vomers without a row of teeth between the vomerine fangs (0), a straight tooththrow running transversely between the vomerine fangs (1), transverse vomerine tooththrow 'v' shaped (2). These character states form an ordered transformation series.

(64) Maxilla and vomer not in contact or in point contact (0), maxilla and vomer forming a suture (1) (Fig. 3).

(65) Width of interpterygoid vacuity pair less than 90% of the length (0), width of pair greater than 90% of the length (1).

(66) Flat ventral surface of the cultriform process (0), lateral surfaces of cultriform process meet to form a midline ventral keel (1).

(67) Posterior end of the ventral surface of the parasphenoid plate without sharp rimmed depressions (0), rounded, widely separated, depressions (pockets) at the posterior end of the ventral surface of the parasphenoid plate, with sharp anterior rims (muscular crests) (1), depressions transversely widened so that the muscular crests approach each other forming transverse ridges (2). State 2 represents a further modification of state 1, so the character is treated as ordered.

(68) Posterior premaxillary teeth of equal size or smaller than the anterior premaxillary teeth (0), posterior premaxillary teeth larger than anterior premaxillary and maxillary teeth (1).

(69) Posteromedial corner of the palatine simple, not extending posterior to the most anterior ectopterygoid tooth (0), elongate posteromedial process of the palatine extending posterior to the most anterior ectopterygoid tooth (1).

(70) Exoccipital and pterygoid not in contact or contact not visible ventrally (0), exoccipital-ptyerygoid suture visible in ventral view (1).

(71) Round patch of denticles on the parasphenoid at the base of the cultriform process (0), parasphenoid denticle field enlarged to a transverse 'belt' extending between the pterygoid-parasphenoid articulations (1), parasphenoid denticles absent (2). These states represent modifications in two different directions away from the plesiomorphic state, therefore the character is treated as unordered.

(72) Parasphenoid plate subrectangular, without lateral 'wings' (0), parasphenoid plate expanded transversely, creating lateral 'wings' (1).

(73) Ventral surface of the cultriform process flat or gently convex (0), ventral surface of the cultriform process with a median keel (1).

(74) Single anterior palatal fossa (0), anterior palatal fossae paired, divided by a median ridge (1).

(75) Lateral margin of the pterygoid, bordering the subtemporal vacuity concave (0), lateral margin of the pterygoid straight in ventral view (1).

(76) Maxilla forming most of the lateral border of choanae (0), lateral processes of vomer and palatine approach one another so as to reduce the maxillary contribution (1), vomer-palatine suture lateral to the choanae excludes maxilla entirely (2). State 1 is clearly intermediate between state 0 and state 2, so the character is ordered.

(77) Vomers with a field of denticles (0), vomers without a field of denticles (1),

(78) Absence of a tooththrow behind the palatine tusks (0), four to six palatine teeth (1), more than eight palatine teeth (2). This character forms a clear transformation series of increasing numbers of palatine teeth.

(79) Medial margin of the choana without teeth (0), medial margin of the choana with a row of teeth (1).

(80) No sulcus behind the pterygoid articulation on the ventral surface the parasphenoid plate (0), Short sulcus becoming wider and deeper postero-laterally, behind the pterygoid articulation (1).

(81) Dorsal surface of the parasphenoid plate without parapterygoid crests (*sensu* Bystrow & Efremov, 1940) (0), dorsal surface of the parasphenoid plate bears parapterygoid crests (1).

(82) The strut of bone that separates the interpterygoid vacuity from the subtemporal fossa consisting entirely of the palatine ramus of the pterygoid (0), invasion of this strut by the ectopterygoid (1).

(83) Posterior edge of the ectopterygoid contributes to the anterior margin of the subtemporal fossa (0), posterior end of the ectopterygoid separated from the subtemporal fossa by an alar process of the jugal (1).

(84) Posterolateral ramus of the vomer not extending posterior to the palatine tusks (0), posterolateral ramus of the vomer extending posterior to the palatine tusks (1).

(85) Ascending ramus of the epipterygoid is a slender rod (0), ascending ramus is robust (1) (Fig. 8).

(86) Pterygoids without ornament (0), ventral surface of the pterygoids with ornament (1).

(87) Pterygoids with denticles (0), pterygoids without denticles (1).

(88) Palatal surface of the premaxillae smooth (0), rugose, medial tubercle on the palatal surface of the premaxillae (1).

Mandibular characters

(89) No extension of the mandible behind the glenoid fossa (0), postglenoid area on the mandible (1) (Fig. 3).

(90) No arcadian groove at the posterior end of the mandible (0), arcadian groove present (1).

(91) Prearticular extending anteriorly, at least as far as the level of the mid point of the middle coronoid (0), prearticular not extending anterior to the level of the suture of the middle and posterior coronoids (1).

(92) Posterior coronoid not visible on the mandible when viewed laterally (0), posterior coronoid raised dorsally so that it is visible in a lateral view of the mandible (1).

(93) Posterior meckelian foramen bordered by the prearticular, postsplenial and the angular (0), posterior meckelian foramen bordered by the prearticular and postsplenial exclusively (1).

(94) Parasymphysial teeth (includes parasymphysial tusks) behind the marginal tooththrow (0), parasymphysial teeth absent (1).

(95) All three coronoids with field of small denticles (0), field of denticles restricted to the posterior coronoid (1), coronoids without any denticle fields (2). The reduction of the extent of the coronoid denticle field forms a clear transformation series and the character is ordered.

(96) Prearticular not extending posterior to the level of the glenoid (0), prearticular extending posterior to the glenoid, covering the medial face of the articular (1).

(97) Mandibular sulcus shallow or absent at its posterior end (0), mandibular sulcus deeply incised at its posterior end (1).

(98) Postglenoid process (if present) on the posterior end of the mandible no longer than the arcadian process (0), postglenoid process much longer than the arcadian process (1).

(99) Postglenoid area of mandible slopes ventrally away from the glenoid socket in lateral view, or is flat topped or with a gentle upward curvature (0), postglenoid area with a transverse trough behind glenoid socket followed by a dorsally bulging tip (1) (Fig. 4).

(100) Chorda tympanic foramen located on the suture between the articular and the prearticular (0), chorda tympanic foramen located on the prearticular alone (1), chorda tympanic foramen absent (2). Presumably the chorda tympanic foramen could be lost at any stage, independant of its position relative to the prearticular, therefore the character is treated as unordered.

(102) Mandible without a hamate process (0), tall hamate process projecting dorsally immediately in front of the antero-medial corner of the glenoid of the mandible (1).

(101) Coronoid bones without teeth other than denticles (0), posterior coronoid with a row of teeth (1), all coronoids with a continuous tooththrow (2). The character forms an ordered transformation series.

Axial skeleton characters

(103) Ventral edges of adjacent intercentra in contact (0), ventral edges of adjacent intercentra prevented from contacting by intervening pleurocentra (1).

(104) Intercentra are dorsally open crescents of bone (0), intercentra are dorsally closed disks or spools (1).

(105) Height of neural spines is greater than the length between the pre- and postzygapophyses (0), height of neural spines less than or equal to the length between the pre- and postzygapophyses (1), height of neural spines less than 40% of the length between the pre- and postzygapophyses (2). These character states form a transformation series of decreasing neural spine height, therefore they are ordered.

(106) Rounded transverse section of the neural spines (0), lateral buttressing of the neural spines creating a cross-shaped transverse section (1).

(107) Less than 26 presacral vertebrae (0), more than 28 presacral vertebrae (1).

(108) Pleurocentra large (at least one third the size of the intercentra) (0) pleurocentra reduced or absent (1)

Appendicular skeleton characters

(109) Interclavicle less than 1.3 times longer than broad (0), interclavicle greater than 1.3 times longer than broad (1).

(110) Clavicular facets on the ventral surface of the interclavicle separated by an intervening strip of ornament (0), clavicular facets in contact anteriorly (1).

(111) Supraglenoid buttress of the scapulocoracoid co-ossified with the coracoid plate, enclosing the supraglenoid foramen (0), supraglenoid buttress not co-ossified with the coracoid plate, changing the supraglenoid foramen into a ventrally open notch (1).

(112) Dorsal process of the clavicle is a simple spike (0), flange with thickened central rib along the anterior edge of the dorsal process (1) (Fig. 7).

(113) Rounded lateral margin of the clavicle (0), sharp keel along the lateral margin of the clavicle, separating the ornamented ventral surface from the unornamented dorsal process (1).

(114) Supinator process part of a crest that is confluent with the deltopectoral crest (0), supinator process is a discrete projection of bone (1).

(115) Ectepicondyle of humerus is a tall and well-developed crest (0), ectepicondyle is a low rounded bump (1).

(116) Radial articulation small and located on the distal end of the humerus (0), radial articulation is a large convex capitellum placed on the ventral surface of the humerus (1) (Fig. 2).

(117) Iliac blade posterodorsally inclined (0), iliac blade vertical (1).

(118) Iliac blade parallel sided (0), iliac blade flared at its proximal end (1).

(119) Intercondylar fossa on the dorsal surface of the distal femur large, deep and sharply defined (0), intercondylar fossa a small shallow vaguely defined depression (1).

Miscellaneous characters

(120) Dorsal osteoderms in the form of imbricating, thin, unornamented bony scales (0), dorsal osteoderms bear ornament and form a tessellating mosaic of armour plates (1).

(121) Ceratobranchials absent or unossified in adults (0), ossified ceratobranchials present in adults (1).

APPENDIX 2

Distribution of character states amongst the terminal taxa of our analysis. Uncertainty, caused by either polymorphism of the terminal taxon, incomplete preservation, or character inapplicability, is treated equally in the analysis and are all coded as a dash

	5	10	15	20	25	30	35	40	45	50	55	60
ancest ^{or}	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000
<i>Isodectes</i>	00001	00- -	10000	-20-0	00101	-1200	00000	10-00	00-0-	00201	12-00	-0001
<i>Acropious</i>	10001	001-0	10000	-2--0	00101	-1200	00000	01-00	0010-	00201	12000	11001
<i>Dvinosaurus</i>	20101	00-0	10001	01100	00101	-020-	00010	10000	00100	00200	02000	11011
<i>Tupilakosaurus</i>	2010-	00--0	11000	-1100	00101	-0201	00000	11-00	00110	0020-	1212-	1101-
<i>Trimerorhachis</i>	00000	00000	00003	-11-0	00001	00101	00000	00-01	00100	00001	00000	10111
<i>Neldasaurus</i>	0000-	000--	01003	-11-0	00000	-0101	00000	00-0-	00-0-	00001	0-000	10010
<i>Tersomilus</i>	11010	00011	10102	00-10	00000	00000	10010	00000	11000	00000	11011	00000
<i>Trematopidae</i>	11010	00011	10101	00-10	00000	01000	10010	01000	11000	00000	01011	00000
<i>Disorophus</i>	11011	0001-	10-02	-0--0	00000	00000	00010	0-100	1-000	00000	--11	00-00
<i>Eryops</i>	10000	11000	10102	00010	00002	00000	00010	00000	00000	00000	01011	00000
<i>Zatrachydidae</i>	10000	11000	10102	-0--0	00002	00001	00010	0-000	000--	00001	0-011	0-000
<i>Sclerocephalus</i>	10000	11000	01000	-10-0	00012	0000-	00010	0-000	001--	0-000	0-000	00110
<i>Chelidepion</i>	10000	110--	01000	-10--	100-2	000-0	00010	--0-	001--	0-00	0-000	00110
<i>Archegosaurus</i>	10001	11-00	01000	00-00	10012	00000	00010	00-00	00-00	00000	0-000	00110
<i>Platyoposaurus</i>	10001	11-00	01010	00-00	10012	0000-	00010	00000	0010-	00001	0-000	00110
<i>Konzhukovia</i>	10001	11100	01010	10-00	00012	00000	00010	00000	0010-	00001	0-01-	00110
<i>Peltobatrachus</i>	10-0-	-1-0-	0-000	-0--2	0000-	0-000	00110	0-00	00100	0000-	1-2-	00--0
<i>Rhinesuchidae</i>	10001	11100	01021	-10-0	00012	00000	10010	0-002	00110	00000	0-02-	10110
<i>Lydekkerina</i>	10001	11100	01011	-11-1	00000	10011	00020	0-001	00110	00001	1-122	10110
<i>Luzocephalus</i>	10001	11100	01000	-1001	00000	001-1	00120	1--01	00110	00001	1-12-	10110
<i>Lapillopsis</i>	10010	11000	01001	-0-01	00000	100-1	000-0	-0001	00110	00001	1-112	00000
<i>Capitosauridae</i>	10011	11100	01021	11200	00002	10011	00020	01002	00110	00001	1-122	10110
<i>Mastodonsaurus</i>	10011	11100	01020	-12-0	00002	10011	00020	0-002	00110	00001	1-12-	10110
<i>Benthosuchus</i>	10001	11100	01021	11200	00002	10011	00020	01002	00110	00001	10122	10110
<i>Thoosuchus</i>	10001	11100	01010	-1000	00002	10011	00020	11-11	00110	00001	1-12-	10110
<i>Trematosauridae</i>	10001	11100	01000	-1000	00002	10-11	00120	11111	00110	00001	1012-	10110
<i>Almasaurus</i>	10001	--100	01013	-1101	01000	10001	00120	0-000	00-10	00001	1-122	10110
<i>Buettneria</i>	10001	11100	01023	11200	01001	10001	00120	00100	00110	00101	1-122	11110
<i>Laidleria</i>	10-11	01100	01001	-10-1	00002	-0201	00021	1-100	0011-	1010-	1-12-	10110
<i>Platysauridae</i>	10011	00100	11002	-1002	00001	-0201	00021	01-00	0011-	10100	1012-	10110
<i>Rhytidosteleidae</i>	10101	11100	0100-	-10-	00001	10101	00120	11-00	00110	00101	10122	10010
<i>Xenobatrachyops</i>	11101	00-10	11001	-1100	00001	-0201	00120	00-00	00110	01201	1212-	10010
<i>Batrachosuchus</i>	10101	0-1-	01001	-1-0-	00001	-0201	00120	1-100	00010	01201	1-12-	11000
<i>Siderops</i>	10101	--00	-10-1	-1-00	0- - -	-0- - -	0-120	01100	00111	01211	1-12-	10010
<i>Keratobatrachyops</i>	10101	11000	01001	-1100	00001	10101	01020	01-00	0011-	01211	10122	10010
<i>Pelorocephalus</i>	10101	11100	01001	-1- - -	00001	10101	01120	0-00	00111	01211	1-12-	11010
Undescribed Genus	2010-	00-10	00000	-1- - -	00101	-1201	-0000	11-00	00-10	-020-	1202-	11110

[illegible]