

Bilaterally symmetric Fourier approximations of the skull outlines of temnospondyl amphibians and their bearing on shape comparison

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Present work illustrates a scheme of quantitative description of the shape of the skull outlines of temnospondyl amphibians using bilaterally symmetric closed Fourier curves. Some special points have been identified on the Fourier fits of the skull outlines, which are the local maxima, or minima of the distances from the centroid of the points at the skull outline. These points denotes break in curvature of the outline and their positions can be compared to differentiate the skull shapes. The ratios of arc-lengths of the posterior and lateral outline of 58 temnospondyl skulls have been plotted to generate a trianguarity series of the skulls. This series grades different families, some of their genera and species as well as some individuals according to their posterior and lateral skull length ratios. This model while comparing different taxa, takes into account the entire arc-length of the outline of the temnospondyl skulls, and does not depend on few geometric or biological points used by earlier workers for comparing skull shapes.

1. Introduction

The study of taxonomy and phylogeny of the extinct vertebrates depends heavily on the morphology of their skulls. The outlines of the vertebrate skulls are variable and they help in recognizing the animals. This is especially true for a group of extinct vertebrates, the temnospondyl amphibians. The temnospondyl skulls are the heaviest part of their skeleton and are better represented in fossil records than the post-cranial elements. The taxonomy of the temnospondyls is greatly based on the features of their skulls (Milner 1994; Damiani and Warren 1996; Yates and Warren 2000; Warren and Marsicano 2000; Schoch and Milner 2000; Damiani 2001). The temnospondyl skull show innumerable variations with all possible combinations of different types of the tabular horns, otic embayments, snout patterns, etc.

The temnospondyl skull outlines, in dorsal view, can be broadly classified into three major shape variants; namely; a semicircle, or an equilateral triangle, or an isosceles triangle

with extended height. The members of the families Dvino-sauridae, Plagiosauridae, Brachyopidae, Chigutisauridae, along with some Actinodontidae and Rhytidosteidae belong to the first type. The Capitosauroida (*sensu* Schoch and Milner 2000), Wetlugasauridae, Benthosuchidae, Thoosuchidae, Lyrocephaliscidae, Metoposauridae, Almasauridae, Indobrachyopidae, Lydekkerinidae, Lapllopsidae and some genera of Rhytidosteidae, Rhinesuchidae, and Arche-gosauridae belong to the second group. Most of the arche-gosaurids and trematosaurids belong to the last type. The posterior part of the skull outlines, in all three types, can be simple or can have notches, bays and/or horns of varied shapes and sizes. However, there are arrays of intermediate shapes of the skull outlines with in the three basic types. Altogether, temnospondyl skull outlines show wide ranges of variations as far as their face elongation and posterior skull boundaries are concerned.

Since the work of D'rcy Thompson (1917) quantitative description and analysis of biological shapes has become

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a topic of interest. Today biological shape-analysis has evolved into a separate branch of science (Zhan and Roskies 1972; Bookstein 1978, 1982, 1986, 1991; Chapman *et al* 1981; Bookstein *et al* 1985; Chapman 1990; Kendall 1989; Temple 1992; Rohlf and Marcus 1993; Lestrel 1996, 1997; Dryden and Mardia 1998). However, no attempt has so far been made to quantitatively analyse the shape of the outlines of the temnospondyl skulls in light of these new methods. It is thus worthwhile to develop a quantitative scheme of description and comparison for the temnospondyl skull outlines that not only preserves the shape details but also remains invariant over skulls of different taxa. The scheme should also be capable of grading these skulls according to their face elongation or according to their posterior curvatures.

The variations in the temnospondyl skull shapes were earlier studied using a number of biological or geometric feature points of the skulls (Colbert and Imbrie 1956; Welles and Cosgriff 1965; Welles and Estes 1969). However, according to O'Higgins, 1997, this approach suffers from the subjectivity in the choice of landmarks, and in its ability to capture the information on the arc length and curvature for the outline reaches between a handful of landmark points. Moreover, in a landmark-based study, it is difficult to maintain a single scheme of landmarking over varied skull shapes – a prerequisite for inter-taxa shape comparison of the temnospondyls. Another group of workers suggest that the elliptical Fourier descriptors (*cf.* Khul and Gardina 1982) are suitable for numerical characterization of closed graphs of complex morphologies, found in biological as well as in abiotic forms (Ehrlich and Weinberg 1970; Kaesler and Water 1972; Zhan and Roskies 1972; Anstey and Delmet 1973; Rohlf and Archie 1984; Ferson *et al* 1985; O'Higgins and Willams 1987; Thomas *et al* 1995; Lestrel 1996, 1997; Ohtsuki *et al* 1997; Jacobshagen 1997; Perugini 2002). Bookstein *et al* (1982) criticized the use of Fourier-based methods for comparing biological shapes as it obscures homologies. However, Read and Lestrel (1986), Ehrlich *et al* (1983) and Temple (1992) discussed the usefulness of Fourier-based methods.

In this paper, we present a methodology for studying the shapes of temnospondyl skull outlines in dorsal view. In order to capture the variations in the intricate details of the temnospondyl skulls we have used Fourier-based approximations for these outlines. These approximations are closed 2D curves, corrected for bilateral symmetry. In the subsequent section we demonstrate how the properties of these approximations can be used to grade and compare the temnospondyl skull outlines by their shape variations.

2. Materials and methods

Temnospondyl fossils have a wide temporal (Permian to Cretaceous) and spatial distribution. Abundant illustrations and descriptions of the skulls of the temnospondyls are

available. Apart from individual descriptions of different taxa by many authors, most of the available temnospondyl skulls are well illustrated in the classical review by Romer (1947) and in the recent review by Schoch and Milner (2000). The temnospondyl skulls are so flat in dorsal view that two-dimensional studies reveal almost all the aspects of the outlines.

For this study, we have chosen 58 skulls of extinct temnospondyls (figures 1, 3, 4). Most of the major taxonomic groups have been incorporated. More than one specimen of a family or genera has been included in few cases to study inter-family/genera variations. We have included some specimens from growth series of few temnospondyl taxa (Warren and Hutchinson 1988; Schoch and Milner 2000; Steyer 2003) to study shape changes through ontogeny. However, in all the cases only the complete or nearly-complete skull outlines well preserved and well illustrated have been selected.

Hand-drawn tracings of published diagrams and photographs of the skulls were digitized using a flatbed scanner and a raster to vector conversion software (Corel Trace) to obtain two-to-four-thousand sequenced data points per outline. Scale invariant Fourier approximations (based on first 40 harmonics) were computed for each outline. These approximations almost exactly match the boundary (where each $R^2 > 0.99$). The first harmonic produces an ellipse that provides the general elongation (ellipticity) of the skull outline. At higher harmonics, more complex and intricate features of the outlines were gradually captured (see also Ferson *et al* 1985). All computations were performed using MATLAB. However, all the 58 specimens lacked bilateral symmetry in greater or lesser degrees due to biological (*cf.* Simmons *et al* 1998) or taphonomic causes. Thus, the approximations are also biased by asymmetry.

Ideally, the skull outlines should be bilaterally symmetrical about their midline sutures. This suture can be approximated by a straight-line that starts from the point of intersection of postperietal suture with the posterior skull boundary (p, figure 2a) and terminates at the anterior margin at the point of intersection with the suture between the premaxillae (q). This suture was also chosen to be the Y-axis of the outline curves, with posterior end as the origin (also, the starting point for Fourier approximations). In order to obtain a Fourier approximation, which is symmetric, we sampled pairs of points on the outline curve, lying on either side of the symmetry axis and at equal arc-length distances from the starting point. From these pair of points, we generated a new set of points on both sides of the symmetry axis that are equidistant from the symmetry axis and have same Y-values (see Annexure). Fourier approximations of these new points generated bilaterally symmetric closed 2D curves (SFA; figure 1).

In the next step we plotted the Euclidian distances of all points on the SFA from their centroid against the arc-

lengths of SFAs. These plots are referred as outline characteristic curves (OCC, figure 1). The local extrema of the OCCs are termed as OCC points. Extremely close spaced OCC points, appearing mostly due to minor irregularities on the outline, were taken as single points.

3. Results and discussion

3.1 OCC points

About 10 OCC points can readily be recognized in the OCCs of most of the outlines. However, the forms without tabular horns show 4 or 6 OCC points, whereas, some

bizarre forms like the dissorophids, zatrachids and some chitisaaurids show more than 10 OCC points. The OCC points generally occur at the two ends of the mid-line suture, at the two sides of the tabular horns and otic notches, squamosal flares and at the beginning of the skull elongation at the lateral margins on the SFAs. Since the SFAs are scale invariant, these points help in comparing similar looking skull outlines.

Among the OCC points, the point at lateral margin is most important. This, in case of average temnospondyl skulls (having 10 OCC points) represent the minimum distance from the centroid. The points usually fall around the

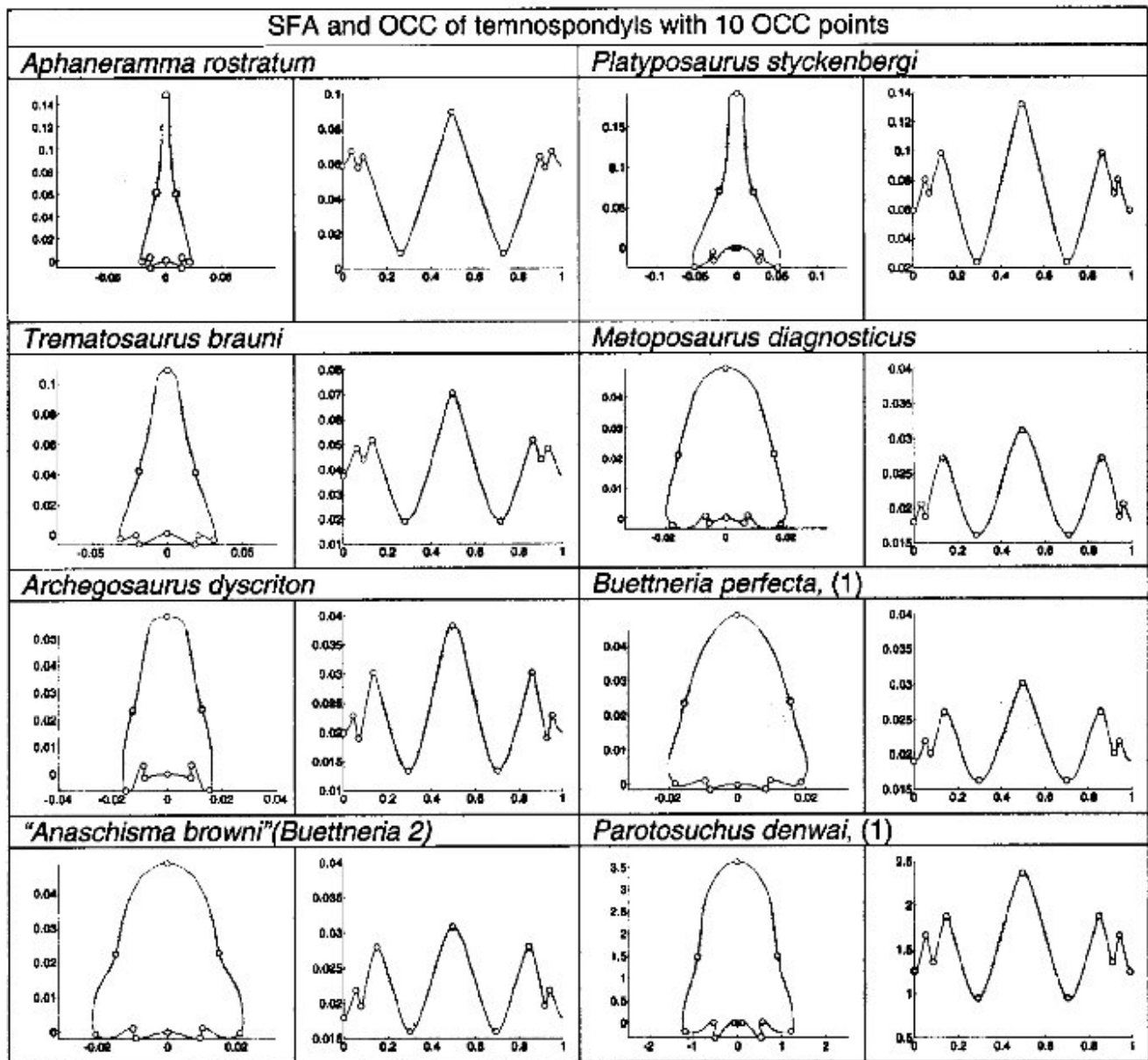


Figure 1. For caption see page No. 385.

suture of jugal and maxilla. In certain cases like in some benthosuchids or in almasaurids the points fall on jugal and in some (like the *Pnematostega*, *Laidleria*, *Uranocentron*, *Scelocephalus*, *Platyposaurus* and *Rhinesuchus*) they fall on the maxilla. The OCC points on the lateral margin of SFA show a break in the curvature pattern at the lateral margin. The dentitions at the ventral side of the skull roof also bear a special relation with that OCC point. Posteriorly, the dentition ends around that point. This means that the dentition would be restricted in the anterior part of the skulls where the mid-lateral OCC points are more anteriorly placed than others. For example, the point is anterior in brachyopids and chigutisaurids than in the capitosaurids. Unlike the capitosaurids, the first two families had

their dentitions restricted at the anterior half of the skull. Hence, the middle part of the lateral side of the temnospondyl skulls is an area of interest. For extreme shapes, however, this does not hold well. The plagiosaurids used in the experiment are so semicircular that their OCC points are not located at the mid-lateral skull, instead they shift towards the anterior tip and represent the curvature of the premaxilla. Schoch and Milner (2000) noted that the variations in skull shapes of the 'stereospondyls' and their dentition are related to the feeding habits. Future research in this field could be supplemented by our finding that the middle lateral skull bears OCC points to mark the change in the overall snout elongation and dentition and hence the change in the habitat.

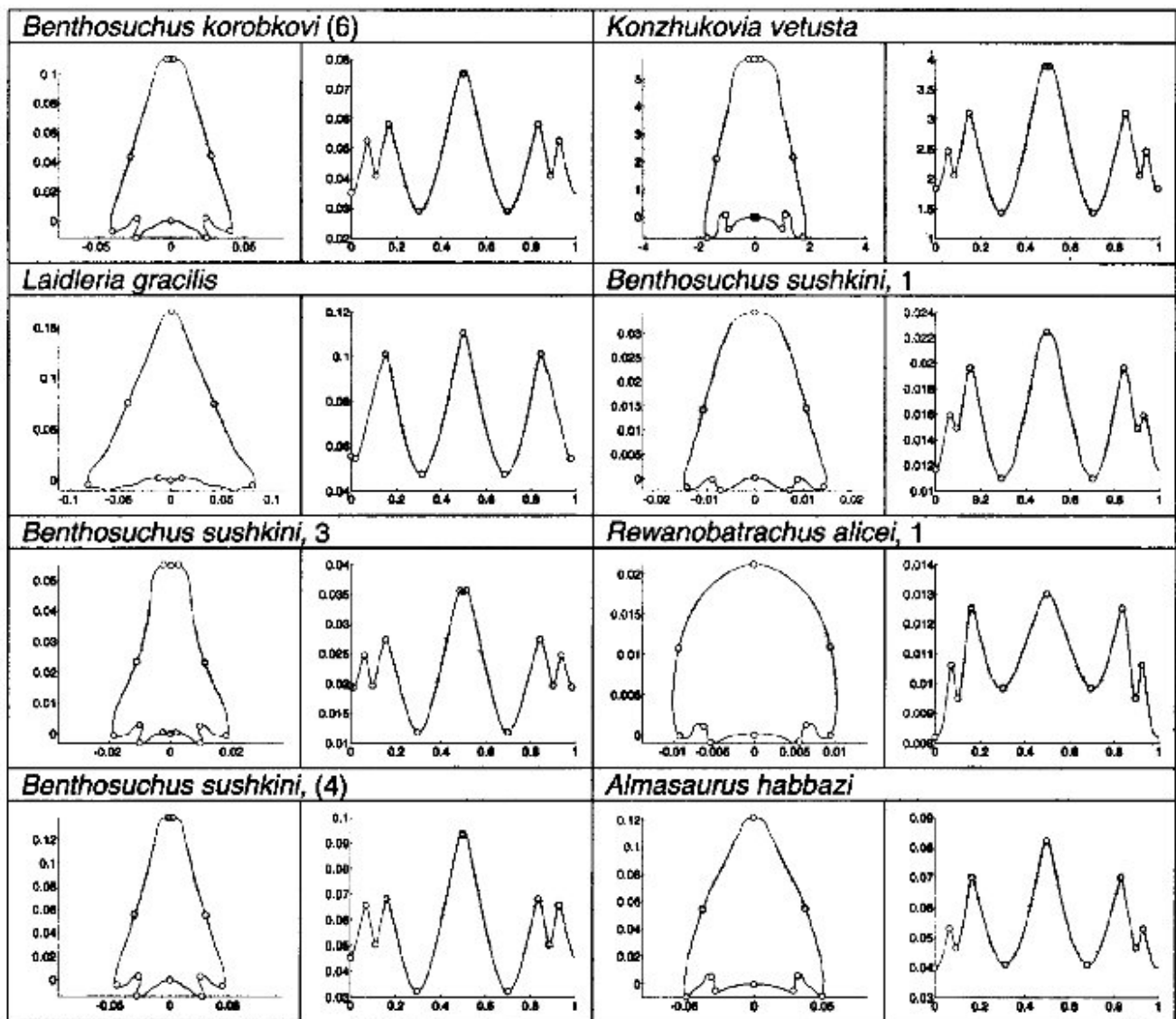


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3.2 Shape grading

The arc-length distances between the starting point and the OCC point at the squamosal (posterior arc-length) when plotted against the distance from latter to the tip of the snout (lateral arc-length), a linear grading is seen from long snouted to semicircular forms (figures 3, 4). As the SFAs are scale-invariant, sum of those two arc-lengths is constant for all the SFAs and hence the ratios plot show a linear grading according to the triangularity of the outlines.

The elongate skulls with moderate tabular horn and shorter posterior width are placed at the left top of the plot and the skulls with short face and wide posterior length at

the right bottom. The series starts with *Aphaneramma* and ends with *plagiosternum* (figure 3). The taxa in between show gradations of triangularities accordingly. However, the skull which do not have tabular horns are usually wider and the arc-length of their posterior boundaries sometimes become close to the some of the forms having pointed tabulars. The projections of the tabular adds to the posterior arc-length of these forms. To avoid this, another plot for the forms without tabular horns have been shown (figure 4). However, certain problems still exist in the gradation plot. The *Cyclotosaurs* outline behave like the ones without tabular horn and *Mordex* (Milner and Sequeira 2003) with an unusually flared posterior boundary groups with the

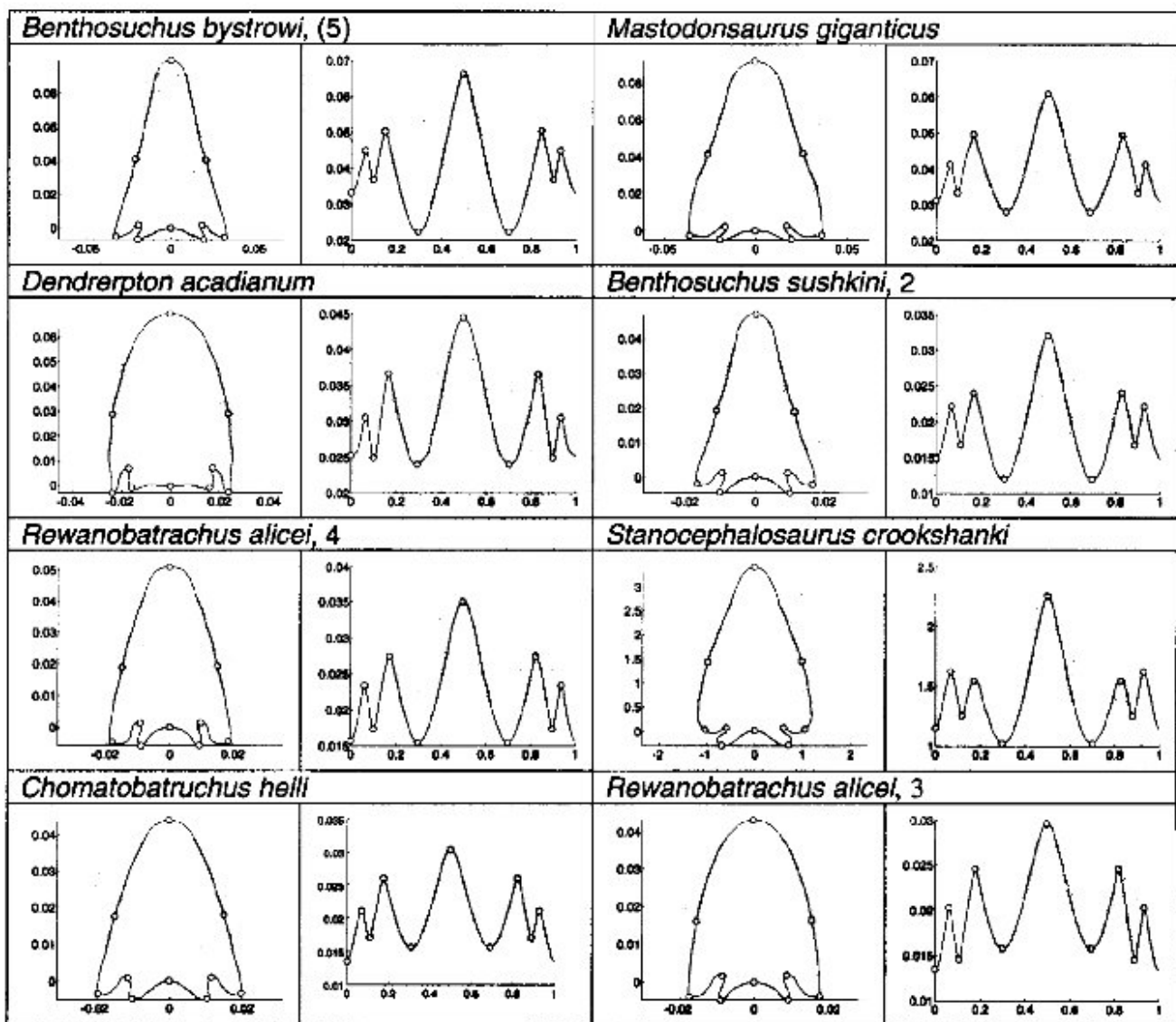


Figure 1. For caption see page No. 385.

plagiosaurids. The plotting of these two is problematic and does not bear any significance. *Doleserpeton* (Bolt 1977) also have high value of lateral arc-length and are grouped with trematosaurids, which is an aberration. Few skull outlines having more than 10 OCC points (see figure 1) are not included in the above plot. These outlines have more than one squamosal or lateral OCC points that make the posterior and lateral arc-lengths indeterminable.

Aphaneramma, *Platyposaurus* and *trematosaurus* fall into groups which have highly elongate skulls and shorter width with tabular horns. The metoposaurids and almasaurids are plotted as the next 'elongated' group with wider posterior margin and moderate tabular horns. Then

come the *Mastodonsaurus*, some benthosuchids, parotosuchids and *Konzhokova* (Gubin 1991). These have wider posterior arc-length and prominent tabular horns and moderate skull elongation. *Stanocephalosaurus*, *Chomatobatrachus*, some rhinesuchids, a species of *Wetlugasaurus*, *Uranocentron*, *Watsonisuchus*, *Rewanobatrachus* and *lapillopsis* come next with lesser elongate skulls and wider posterior margin with prominent tabular extensions. These are followed by the plagiosaurids with their short and parabolic skulls. For the skulls without tabular horn (figure 4) the 'triangularity series' starts with *Neldasaurus*, then through *Eryops*, *Mahavisaurus*, *Laidleria*, *Xenobrachyops*, *Brachyops* and *Vigilius* it ends with the plagiosaurids.

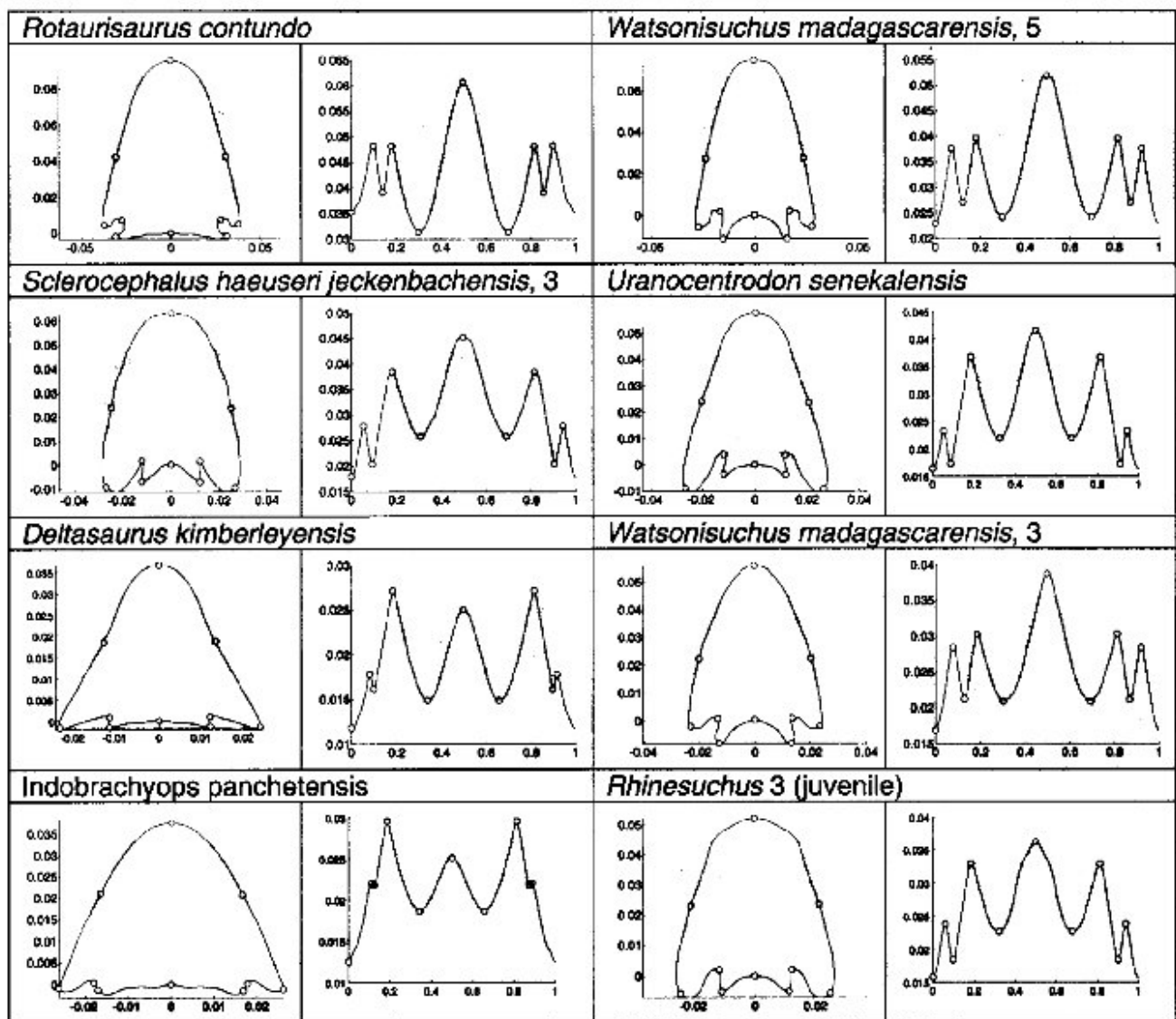


Figure 1. For caption see page No. 385.

3.3 Shape of OCC and organization of OCC points

Figure 1 indicates the SFA (with the OCC points) of many of the temnospondyl skull outlines. The position of the OCC points and the shape of the OCC are different in lonchorhynchine trematosaurids and the short faced plagiosaurids. For semicircular forms the OCC are 'M' shaped while for the others (that is the long snout bearing and the triangular forms) they are 'W' shaped (that is inverted). Among the 'W' type, the extremely long snout bearing *Aphaneramma* shows one very pronounced maxima (a prominent OCC point) at the snout. This separates the extremely long snout bearing lonchorhynchine forms from other long

snout bearing types. The distinction of those extreme shapes is easy and may be done by eye estimations only. However, the comparison of skull shapes of similar looking temnospondyl families is not easy. This can be done using the SFA and the OCCs.

For example, at the family level, the SFA and OCC as well as the position of the OCC points are different for the metoposaurids and the capitosaurids. The latter has OCC point at the tip which is more pronounced (figure 1). The OCC points are variable among the different genera of those families. An example of shape comparison at generic level may be the metoposaurids. The comparison of skull shapes among different genera of metoposaurids is a long standing problem (Colbert and Imbrie 1956; Roychowdhury

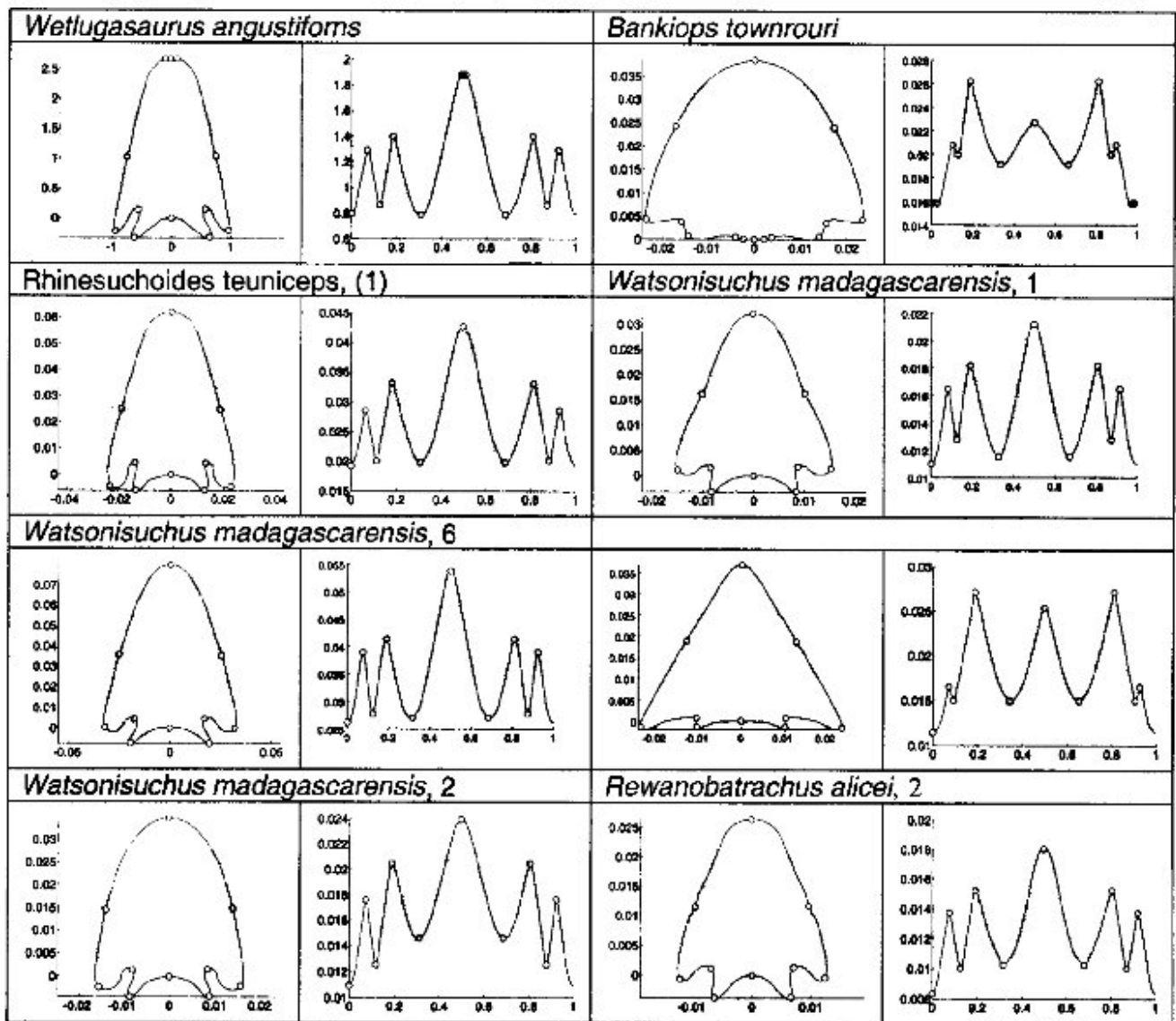


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1965; Hunt 1993; Sengupta 2002). The elongation of the anterior part of the skull and the curvature of the tabular horns vary among the metoposaurids. The variation is small

but taxonomically significant. The SFA of the skull outlines (with OCC points) of *Metoposaurus diagnosticus* and *Buettneria perfecta* (Hunt 1993) as well as '*Anaschisma*'

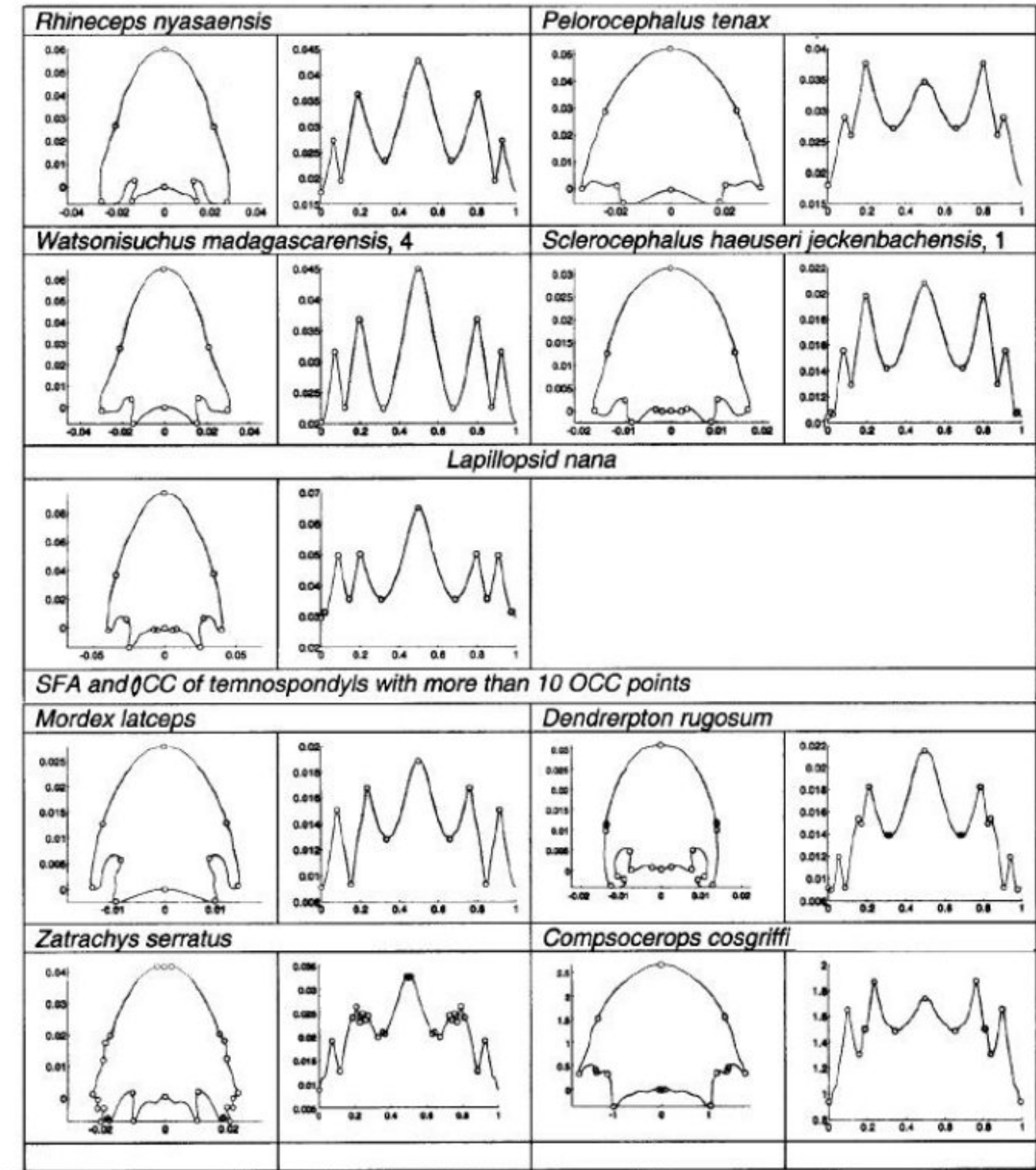


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(Branson and Mehl 1929) when compared show the differences in the position of the OCC points at the tabular horn, otic notch and at the lateral margin. The lateral point is most posterior and tabular point is closest to the start-

ing point in *M. diagnosticus*. The squamosal point is widest and the orbits are closest to the lateral point in '*Anaschisma*'. These small variations are noticeable in their respective OCCs.

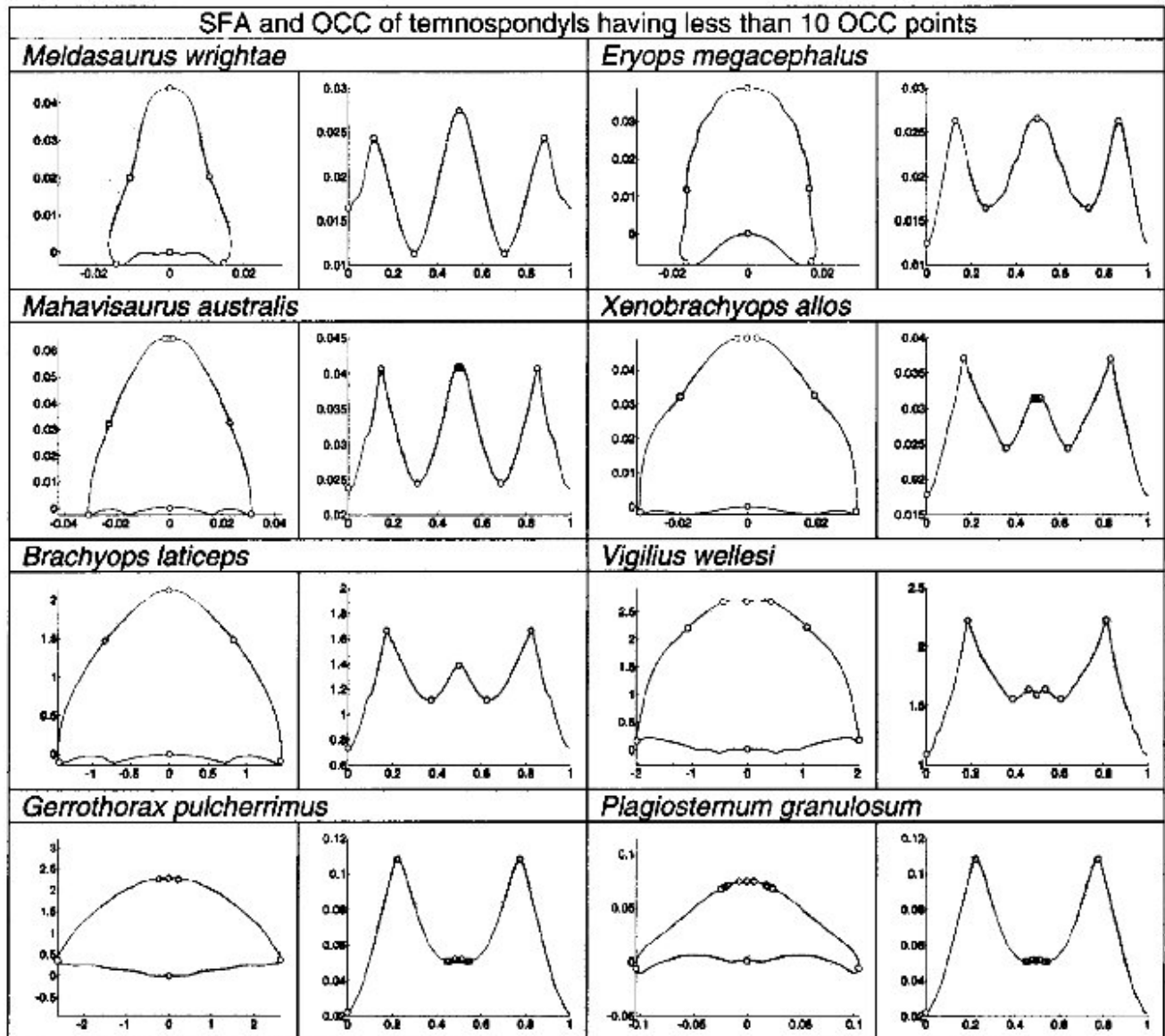


Figure 1. The SFA of the skulls of some temnospondyl amphibians along with their OCC. The origins of the two dimensional OCC plots are manipulated to provide equal area for the plots. This is for the sake of ready comparison of the curves. The OCC points are marked by open circles. Different species have numbers within parenthesis, which correspond to figures 3 and 4. The individuals of progressive growth series of a taxon are indicated by increasing numbers without parenthesis. This also corresponds to figures 3 and 4. Illustrations taken from Branson and Mehl (1929), Bolt (1977), Boy (1988), Carrol (1988), Cosgriff (1974), Cosgriff and Zawiskie (1979), Damiani and Warren (1996), Dutuit (1976), Gubin (1991), Marsicano (2000), Mukherjee and Sengupta (1998), Milner (1980), Milner and Sequeira (2003), Romer (1947), Riabinin (1930), Scoch and Milner (2000), Sengupta (1995), Shishkin (1987), Steyer (2003), Swain (1941), Warren (1995), Warren and Hutchinson (1988), Warren and Marsicano (2000), Welles and Cosgriff (1965) and Welles and Estes (1969).

3.4 Growth series

Two adult rhinesuchids, *Rhinesuchoides tenuiceps* and *Rhineceps nyasaensis* with considerable variations in the

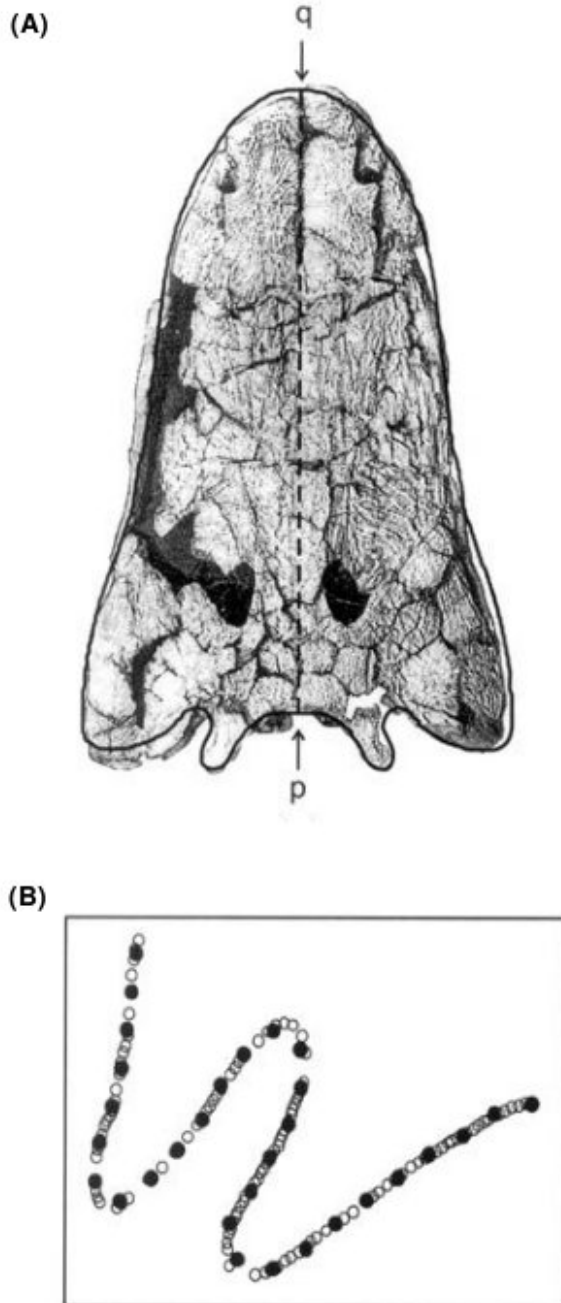


Figure 2. (A) SFA superimposed on the specimen of *Parotosuchus denwai*. The broken line p, q represents the axis of symmetry. (B) Non-uniformly placed data points from scanned outlines (open circles) vs. equispaced, standardized outline data (solid circles) shown for the posterior-lateral part of *Wetlugasaurus angustiformis*.

skull outlines and a juvenile of *Rhinesuchus* (Schoch and Milner 2000) is considered in the study. The juvenile has similar lateral and posterior arc-lengths (when put to same scale) with *Wetlugasaurus angustiformis* (Riabinin 1930). The three, however, are plotted in close position with *Rhineceps nyasaensis* having higher posterior arc-length and lesser lateral arc-length. Another growth series, that of the *Watsonisuchus madagascarensis* (Steyer 2003) has also been plotted. All the individuals of six growth stages are plotted in close clusters. Their position is at the 'higher posterior arc-length, lower lateral arc-length' position together with the rhinesuchids and the three individuals (of progressive growth stages) of actinodontids like *Sclerocephalus haeuseri jeckenbachensis*, Boy 1988 (Schoch and Milner 2000). Several individuals of *Benthosuchus sushkini* (of different growth stages, see Schoch and Milner 2000), and few adults of different species of benthosuchids like *B. sushkini*, *B. bystrowi* and *B. korobkovi* (Schoch and Milner 2000) have been studied. They are plotted between the metoposaurids and the *Watsonisuchus*, *Rhinesuchus*, *Sclerocephalus* cluster in figure 3. Interestingly, the lateral and posterior arc-length ratio of the first and last individuals of the growth stages of *Benthosuchus sushkini* is same. This is also true for *Watsonisuchus madagascarensis*. However, the plots of different growth stages of *Rewanobatrachus alicei* (Warren and Hutchinson 1988) in figure 3 are varied and cluster with different families of temnospondyls. Outline wise, the different growth stages of *R. alicei* are most varied and have affinities towards the skull outlines of some benthosuchids, *Rotaurisaurus*, *Watsonisuchus* and *Sclerocephalus*.

4. Concluding remarks

Temnospondyl skull outlines with all the details of their shapes can be represented by symmetrized Fourier approximations (SFA). The approximations are free from taphonomic and other aberrations, as they are bilaterally symmetrized. They are shape invariant and can be compared with other known taxa. Comparison can be done by using the outline characteristic curves and by the position of the OCC points. Comparison can also be done using posterior and lateral arc-lengths of the outlines. The Fourier approximates of the skull outlines may describe homoplasy. However, with in known taxonomic groups it is found useful in comparing shapes. The OCC points discussed in this study are not 'Landmarks' by definition nor are they similar to the feature points used by Welles and Cosgriff (1965). They are the least or most distant points on the outline (SFA) from the centroid. It is possible to identify them through SFAs across a large number of specimens of several temnospondyl taxa.

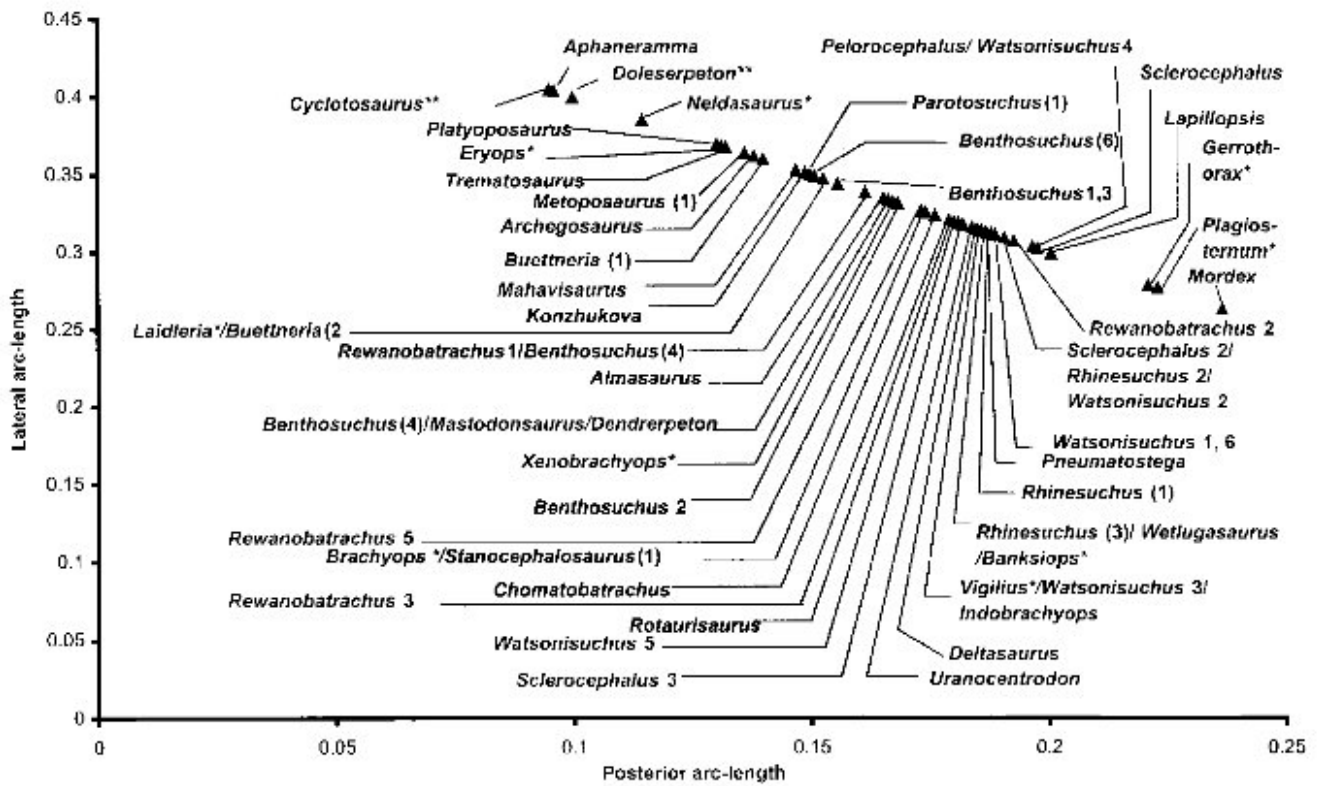


Figure 3. Plot of posterior (X) and lateral (Y) arc lengths of some temnospondyl taxa. See figure 1 for specific names. Taxa marked by double asterisks (**) are not included in figure 1 (see the reason cited in the text). Taxa marked by single asterisks (*) are plotted separately in figure 4.

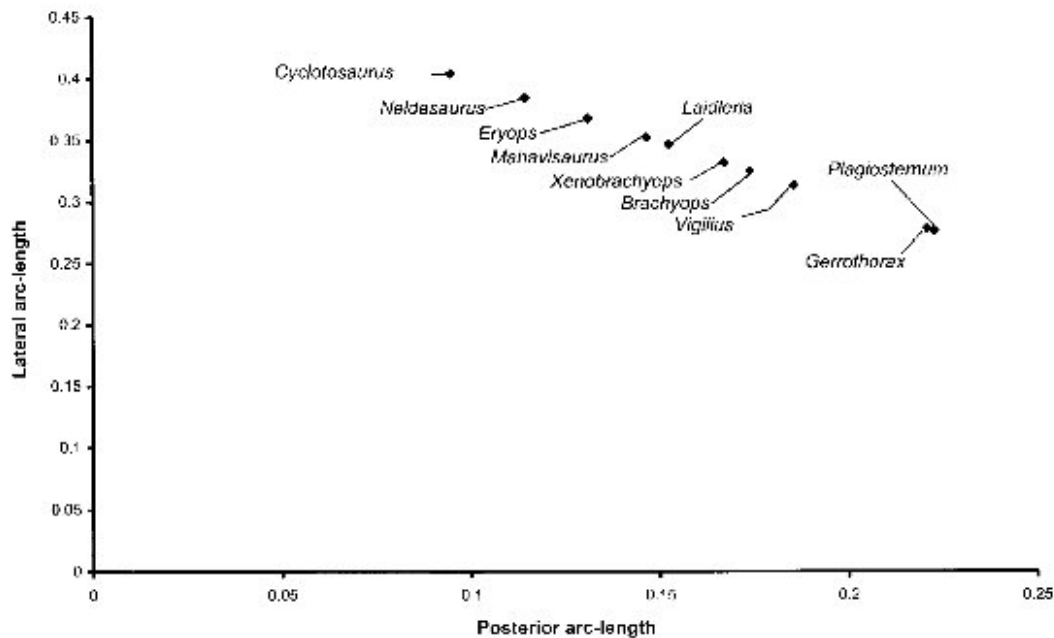


Figure 4. Plot of posterior (X) and lateral (Y) arc lengths of the temnospondyl taxa without tabular horns only. See figure 1 for specific names.

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Annexure

(i) Elliptical Fourier descriptors and arc-length parameterization

Elliptical Fourier descriptors of closed curves in plane (2D) are given by parametric equations

$$S_K(t) = \begin{pmatrix} S_{K1}(t) \\ S_{K2}(t) \end{pmatrix} = \begin{pmatrix} a_{0,1} \\ a_{0,2} \end{pmatrix} + \sum_{k=1}^K \begin{bmatrix} a_{k,11} & a_{k,12} \\ a_{k,21} & a_{k,22} \end{bmatrix} \begin{pmatrix} \cos \omega_k t \\ \sin \omega_k t \end{pmatrix}, \quad (1)$$

for suitable Fourier coefficients a_{kij} 's, truncation K and $\omega_k = 2\pi k$. The indexing parameter $t \in [0, 1]$. That the algebraic formula in (1) is not unique (although the actual 2D curve is) can be readily seen from the following arguments. By a reparameterization of (1) we mean a re-indexing of S_K as $S_K(\phi(t))$ where $\phi: [0, 1] \rightarrow [0, 1]$ is smooth and strictly monotonic. Thus, a reparameterization of the algebraic formula in (1) does not alter the original curve geometrically. A special choice of ϕ , called the arc-length parameterization, is of special interest to us. For any parameterization t it can be shown that the following parameterization formula is unique (up to the starting point, $S_K(0)$).

$$s = \int_0^t (S'^2_{K1}(u) + S'^2_{K2}(u))^{1/2} du$$

is called the arclength parameter and it is characterized by the fact that the tangent vector $(S'_{K1}(s), S'_{K2}(s))$ is of unit length at each point on the Fourier descriptor under s . If we represent (1) through s , the Fourier coefficients can be assigned unique geometric meaning. Therefore, without loss of any generality we can assume that a Fourier descriptor in (1) is parameterized by s (cf. O'Neill 1966).

(ii) Starting point of arc-length parameterization

The problem of choosing an appropriate starting point ($s = 0$) can be solved in an unambiguous manner if the curve given by (1) has natural bilateral symmetry. Suppose the symmetry axis cuts the curve at s_0 and s_1 respectively. Then, either of these two points can be chosen as unique starting point of the parameterization. For temnospondyl skulls we can further differentiate between s_0 and s_1 as one of them (say, s_0) must fall in the lower part of

the skull. By suitable congruence transformations we can place the skull so that $S_K(s_0)$ is the origin of the coordinate system and the symmetry axis joining $S_K(s_0)$ and $S_K(s_1)$ is the positive Y axis. Call the resulting 2D curve S_K^* . Now, we have a unique algebraic formula of the Fourier descriptor of the skull boundary, namely, $S_K^*(s - s_0)$. The Fourier descriptor given by (1) has further simplification under the assumptions of bilateral symmetry. Straight-forward geometric arguments show that $S_{K1}^*(s)$ is an odd function while $S_{K2}^*(s)$ is an even function. Therefore, the final Fourier coefficients will satisfy symmetry constraints, namely,

$$a_{0,1}^* = a_{0,2}^* = 0 \quad a_{k,11}^* = a_{k,22}^* = 0 \quad \text{for } 1 \leq k \leq K. \quad (2)$$

Further, the condition $\sum_{k=1}^K (a_{k,12}^2 + a_{k,21}^2) = 1$ has to be imposed for scale standardization of various samples.

(iii) Energy-phase summary of Fourier coefficients

After analysing several samples we find the following two statistics to be analytically most informative.

$$\text{Energy at } k\text{th harmonics} = a_{k,12}^2 + a_{k,21}^2.$$

$$\text{Energy partition phase at } k\text{th harmonics} = \cos^{-1} \left(a_{k,12} / (a_{k,12}^2 + a_{k,21}^2)^{1/2} \right).$$

The energy and phase together contain the total information of the Fourier descriptor. Finally, it should be mentioned that any smooth closed curve can be approximated by a Fourier descriptor within any level of accuracy by increasing K .

(iv) Discrete Fourier transform computation for bilaterally symmetric closed curves

For a discrete sample $z_i = (x_i, y_i)$, $0 \leq i \leq N-1$, ($N = 2L+1$) from a smooth and closed 2D outline, initially we use the parameterization $z_i \approx S_K(i/N)$ for $0 \leq i \leq N-1$. The resulting Fourier approximation is called Discrete Fourier Transform (DFT). For DFT to work we must have $K \leq (N-1)/2$ as $(\cos(\omega_k i/N), 0 \leq i \leq N-1)$ and $(\sin(\omega_k i/N), 0 \leq i \leq N-1)$ form an orthogonal basis as k runs between 1 and $(N-1)/2$. The Fourier coefficients can be estimated by the Least square method. It can be readily seen that the predicted locations, \hat{z}_i , are given by

$$\hat{z}_i = \sum_{\ell=0}^{N-1} \hat{\vartheta}_{i\ell} z_\ell,$$

for $0 \leq i \leq N-1$, with suitable coefficients $\hat{\vartheta}_{i\ell}$ satisfying $\sum_{\ell} \hat{\vartheta}_{i\ell} = 1$ for each i . This establishes invariance under congruence for the DFT method. DFT can be computed very efficiently using the Fast Fourier transform algorithm.

In the next step of the algorithm we estimate the tangent vectors from (1) at i/N and derive an estimate of the

arclength parameterization, \hat{s} . Using this estimate equispaced points are chosen from the outline (same number for each sample). These points are treated as regularized observations from the outline. Next, the symmetry axis is considered and s_0 and s_1 above are identified as appropriate indices in the sequence of regularized observations. In the final step of symmetrization, arclength parameterization of the left and right hand sides of the symmetry axis are compared. Due to various possible fluctuations these are not identical. A simple proportional-to-arclength matching of the left and right hand sides are performed to generate a consensus symmetric sample from the outline. The last step can be accomplished as follows. Suppose that $0 \leq s \leq c$ and $c \leq s \leq 1$ denote the left and right hand side of the outline respectively. From symmetry considerations we know that for $0 \leq u \leq 1$, $S_K^*(cu)$ and $S_K^*(1 - (1 - c)u)$ are symmetric about Y axis (as per construction). In actuality these are not exactly symmetrically placed. As part of symmetrization process we force these two points to become symmetric about Y axis (by averaging and differencing the coordinates). As a result, we obtain an exactly symmetric outline by varying $0 \leq u \leq 1$.

Reference

- Anstey R L and Delmet D A 1973 Fourier analyses of zoological shapes in fossil tubular bryozoans; *Geol. Soc. Am. Bull.* **84** 1753–1764
- Bookstein F L 1978 The measurement of biological shape and shape change; *Lecture notes in bio-mathematics* 24 (New York: Springer)
- Bookstein F L 1982 Foundations of morphometrics; *Annu. Rev. Ecol. Syst.* **13** 341–470
- Bookstein F L 1986 Size and shape spaces for landmark data in two dimensions; *Stat. Sci.* **1** 181–242
- Bookstein F L 1991 *Morphometric tools for landmark data: Geometry and biology* (Cambridge: Cambridge University Press)
- Bookstein F L, Strauss J M, Humpshire Chernoff B, Elder R L and Smith G R 1982 A comment on the uses of Fourier methods in systematics; *Syst. Zool.* **31** 85–92
- Bookstein F L, Chernoff R, Elder J, Humphries J, Smith G and Strauss R 1985 *Morphometrics in evolutionary biology*. Special publication 15 (Philadelphia: The Academy of Natural Science Philadelphia)
- Bolt J R 1977 Dissorophid relationships and ontogeny, and the origin of Lissamphibia; *J. Paleontol.* **51** 235–249
- Boy J A 1988 Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (? Höchstes Karbon-Perm) 1. *Sclerocephalus*; *Paläont. Z.* **62** 107–132
- Branson E B and Mehl M G 1929 Triassic amphibians from the Rocky mountain region; *Univ. Mo. Stud.* **4** 155–255
- Carroll R L 1988 *Vertebrate paleontology and evolution* (New York: Freeman) pp 698
- Chapman R E 1990 Shape analysis in the study of dinosaur morphology; in *Dinosaur systematics perspective and approach* (eds) K Carpenter and P G Currie (Cambridge: Cambridge University Press) pp 21–41
- Chapman R E, Glaton P M, Sepkoski J J Jr and Wall W P 1981 A morphometric study of the cranium of the pachycephalosaurid dinosaur *Stegoceras*; *J. Paleontol.* **55** 608–618
- Colbert E H and Imbrie J 1956 Triassic metoposaurid amphibians; *Bull. Am. Mus. Nat. Hist.* **110** 399–452
- Cosgriff J W 1974 The Lower Triassic Temnospondyli of Tasmania; *Geol. Soc. Am. Special Papers* **149** 1–134
- Cosgriff J W and Zawiskie J M 1979 A new species of the Rhytidosteidae from the Lystrosaurus zone and the review of the Rhytidosteidae; *Palaeontol. Afr.* **22** 1–27
- Damiani R J 2001 A systematic revision and phylogenetic analysis of Triassic Mastodonsauroids; *Zool. J. Linnean Soc.* **133** 379–482
- Damiani R J and Warren A A 1996 A new look at members of the Superfamily Brachyopoidea (Amphibia, Temnospondyli) from the Early Triassic of Queensland and a preliminary analysis of brachyopoid relationships; *Alcheringa* **20** 277–300
- Dryden I L and Mardia K V 1998 *Statistical shape analysis* (London: John Wiley)
- Dutuit J M 1976 Introduction à l'étude paléontologique du Triassic Continental marocain. Descriptions des premiers stegocephales recueillis dans le Couloir d'Argana (Atlas occidental); *Mem. Mus. Nat. Hist. Nat. Paris* **36** 1–253
- Ehrlich R, Phaas R B Jr and Healy-Williams N 1983 Comments on the validity of Fourier descriptors in systematics.: A reply to Bookstein *et al*; *Syst. Zool.* **32** 302–306
- Ehrlich R and Weinburg B 1970 An exact method for characterisation of sand shape; *J. Sediment. Petrol.* **40** 205–212
- Ferson S, Rohlf J F and Koehn R K 1985 Measuring shape variation of two dimensional outlines; *Syst. Zool.* **34** 59–68
- Gubin Y M 1991 Permian archegosauroid amphibians of the USSR; *Trudy Pal. Inst. Akad. Nauk. SSSR* **249** 1–138 (in Russian)
- Hunt A P 1993 Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from Western North America: In Aspects of Mesozoic geology and paleontology of the Colorado Plateau; *Mus. North. Arizona Bull.* **59** 67–97
- Jacobshagen B 1997 Craniofacial variability in the Hominoidea; in *Fourier descriptors and their applications in biology* (ed.) P Lestrel (Cambridge: Cambridge University Press) pp 227–249
- Kaesler R L and Waters J A 1972 Fourier analysis of the ostracod margin; *Bull. Geol. Soc. Am.* **83** 1169–1178
- Kendall D 1989 A survey of the statistical theory of shape; *Stat. Sci.* **4** 87–120
- Kuhl F P and Gardina C R 1982 Elliptical Fourier features of a closed contour; *Comp. Graph. Image Process.* **18** 236–258
- Lestrel P E 1996 Fourier descriptors in 21st century; in *Fourier descriptors and their application in biology* (ed.) P Lestrel (Cambridge: Cambridge University Press) pp 480
- Lestrel P E 1997 Introduction and overview of Fourier descriptors; in *Fourier descriptors and their applications in biology* (ed.) P Lestrel (Cambridge: Cambridge University Press) pp 22–44
- Marsicano C A 2000 Chigutisaurid amphibians from the Upper Triassic of Argentina and their phylogenetic relationships; *Palaeontology* **42** 545–565
- Milner A R 1980 The temnospondyl amphibian *Dendrerpeton* from the Upper Carboniferous of Ireland; *Palaeontology* **23** 125–141
- Milner A R 1994 Upper Triassic and Jurassic amphibians, fossil record and phylogeny; in *In the shadow of the dinosaurs: Early Mesozoic Tetrapods* (eds) N C Fraser and H-D Sues (Cambridge: Cambridge University Press) pp 5–22
- Milner A R and Sequeira S E K 2003 Revision of the Amphibian genus *Limnerpeton* (Temnospondyli) from the Upper Carboniferous of the Czech Republic; *Acta Palaeontol. Polonica* **48** 123–141
- Mukherjee R N and Sengupta D P 1998 New capitosaurid amphibians from the Triassic Denwa Formation of the Satpura Gondwana basin, central India; *Alcheringa* **22** 317–327

- O'Higgins P 1997 Methodological issues in the description of forms; in *Fourier descriptors and their applications in biology* (ed.) P Lestrel (Cambridge: Cambridge University Press) pp 74–105
- O'Higgins P and Williams A T 1987 An investigation into the use of Fourier coefficients in characterizing cranial shapes in primates; *J. Zool. Soc. London* **211** 409–430
- Ohtsuki F, Lestrel P, Uetake T, Kazutaka A and Hanihara K 1997 Fourier analysis of size and shape changes in the Japanese skull; in *Fourier descriptors and their applications in biology* (ed.) P Lestrel (Cambridge: Cambridge University Press) pp 210–226
- O'Neill B 1966 *Elementary differential Geometry* (New York: Academic Press)
- Perugini D 2002 MorphoUt 1.0: utilities for closed shape morphometry; *Comp. Geosci.* **28** 73–79
- Read D W and Lestrel P E 1986 Comment on uses of homologous-point measures in systematics: a reply to bookstein *et al*; *Syst. Zool.* **35** 241–253
- Rohlf J F and Archie J W 1984 A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae); *Syst. Zool.* **33** 302–317
- Rohlf J F and Marcus L F 1993 A revolution in morphometrics; *Trends Ecol. Evol.* **8** 129–132
- Riabinin A N 1930 A labyrinthodon stegocephalian *Wetlugasaurus angustiformis* nov. gen. Nov. sp. from the lower Triassic of Vetluga-land in northern Russia; *Ann. Soc. Pal. Russie* **8** 49–76
- Romer A S 1947 Review of the Labyrinthodontia; *Bull. Mus. Comp. Zool., Harvard* **99** 3–368
- Roychowdhury T K 1965 A new metoposaurid amphibian from the upper Triassic Maleri Formation of Central India; *Philos. Trans. R. Soc. London B* **250** 1–52
- Schoch R R and Milner A R 2000 Stereospondyli; in *Encyclopedia of Paleo-herpetology* (ed.) P Wellnhofer (München: 3b, Verlag) pp 1–203
- Sawin H J 1941 The cranial anatomy of *Eryops megacephalus*; *Bull. Mus. Comp. Zool. Harvard* **88** 405–464
- Sengupta D P 1995 Chigutisaurid temnospondyls from the Late Triassic of India and a review of the family Chigutisauridae; *Palaeontology* **38** 313–339
- Sengupta D P 2002 Indian metoposaurid amphibians revised; *Paleontol. Res.* **6** 41–65
- Shishkin M A 1987 The evolution of early amphibians (Plagiosauroidae); *Trudy Pal. Inst. Akad. Nauk. SSSR* **225** 1–143 (in Russian)
- Simmons L W, Tomkins J L, Kotiaho and Hunt J 1998 Fluctuating paradigm; *Proc. R. Soc. London B* **266** 593–595
- Steyer J S 2003 A revision of the early Triassic "Capitosaurus" (Stegocephali, Stereospondyli) from Madagascar, with remark on their comparative ontogeny; *J. Vertebr. Paleontol.* **23** 544–555
- Temple J T 1992 The process of quantitative methods in paleontology; *Palaeontology* **35** 475–484
- Thomas M C, Wiltshire R J and Williams A T 1995 The use of Fourier descriptors in the classification of particle shape; *Sedimentology* **42** 635–645
- Thompson D W 1917 *On growth and form* (Cambridge, London)
- Welles S P and Cosgriff J W 1965 A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi*, n. sp. from the Wupatki Member of the Moenkopi Formation of Northern Arizona; *Univ. Calif. Publ. Geol. Sci.* **54** 1–148
- Welles S P and Estes R 1969 *Hadrokkosaurus bradyi* from the upper Moenkopi Formation of Arizona, with a review of the brachyopid labyrinthodonts; *Univ. Calif. Publ. Geol. Sci.* **84** 1–56
- Warren A A 1995 *Plagiosternum granulosum* Fraas: a plagiosaurid temnospondyl from the Middle Triassic of Crailsheim, Germany; *Stuttg. Beitr. Naturkd. Series B*, No. 229, p. 8
- Warren A A and Hutchinson M N 1988 A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of capitosaurid skull; *Palaeontology* **31** 857–876
- Warren A A and Marsicano C 2000 A phylogeny of the Brachyopodea (Temnospondyli, Stereospondyli); *J. Vertebr. Paleontol.* **20** 462–483
- Yates A M and Warren A A 2000 The phylogeny of the 'higher' temnospondyls (Vertebrata, Choanata) and its implications for the monophyly and origins of the Stereospondyli; *Zool. J. Linnaean Soc.* **128** 77–121
- Zahn C T and Roskies R Z 1972 Fourier Descriptors for plane closed curves; *IEEE Trans. Comp.* **C21** 269–281

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