Title: Patterns In Palaeontology: Old Shapes, New tricks – The Study of Fossil Morphology
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Volume: 3
Article: 2
Page(s): 1-10
Published Date: 01/02/2013
PermaLink: http://www.palaeontologyonline.com/articles/2013/patterns-in-palaeontology-old-shapes-new-tricks-the-study-of-fossil-morphology/

CITATION OF ARTICLE

Please cite the following published work as:

Bennett, Verity. 2013. Patterns In Palaeontology: Old Shapes, New tricks – The Study of Fossil Morphology, Palaeontology Online, Volume 3, Article 3, 1-10.

Patterns In Palaeontology: Old Shapes, New Tricks — The Study of Fossil Morphology

by Verity Bennett[*1]

Introduction:

The size and shape of an organism is the product of genetics and environment. It is the raw material on which the process of natural selection (survival of particular animals over others) acts, and so is of central interest in studies of the evolution of ancient forms of life for which DNA information is not available. Fossil morphology, or shape, is the basis of most palaeontological studies, be they describing new species or making deductions about the animal's lifestyle. Phylogenetic studies, those that place species in groups depending on how closely they are related to each other, are based on the presence and absence of particular features. This works on the theory that the more closely related two animals are, the more features they are likely to have in common. Fossil morphology also plays a major role in informing palaeontologists about the ecology of an animal, because form often reflects function. Details of diet, habitat, the way animals moved and the forces that parts of the body could withstand can all be investigated by studying morphology.

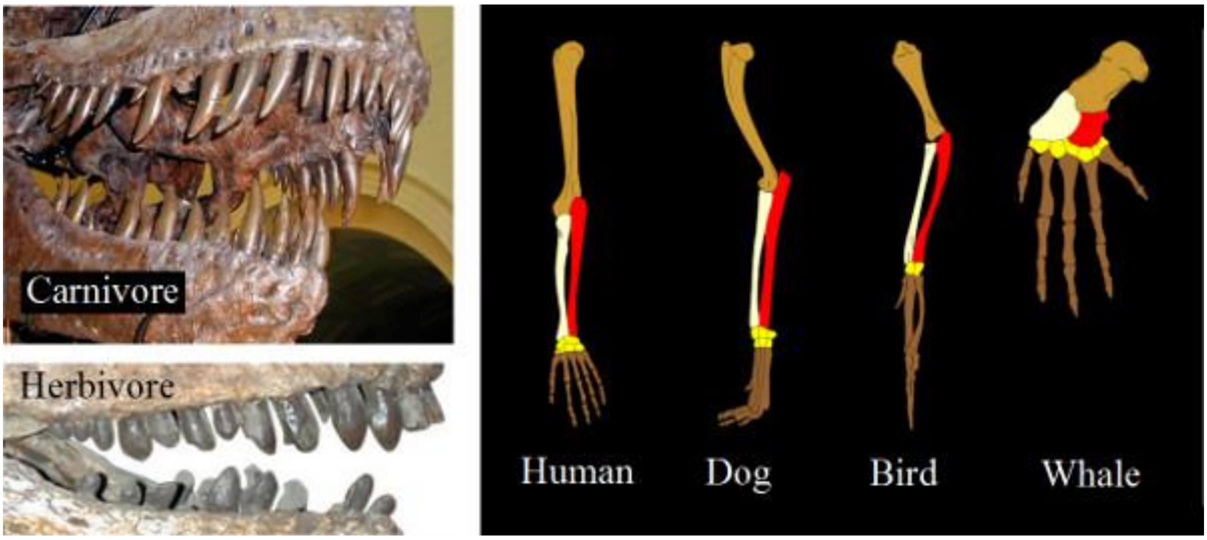

Figure 1 — Top left: sharp, serrated, recurved teeth of a carnivorous dinosaur (Tyrannosaurus, source, copyright Andrew A. Skolnick); bottom left: the short, peg-like teeth of a herbivorous dinosaur (Camarasaurus,source). Right: different mammalian limb shapes for (left to right) grasping, running, flying and digging (source).

Connected changes in the morphology of different parts of a biological structure can reflect developmental or evolutionary mechanisms that act on these parts together. Groups of parts that are affected together are often referred to as modules, and they give clues as to the limitations or freedoms of the mechanism that produced the animal diversity.

Collecting Shape Data:

Traditionally, morphology has either been described qualitatively or measured by collecting data sets of lengths, ratios and angles. However, in recent years, rapid advances in technology, computer power and analytical methods have led to the increased use of digital-imaging methods. These include photography, photogrammetry, microscribing, laser scanning and computed tomography (CT) scanning. Such techniques vary a great deal in terms of cost and speed, and how suitable they are depends on the research question.

Photography: Two-dimensional (2D) morphology can easily be — and has traditionally been — captured by photographing objects from the same relative plane of view. It is cheap (compared with other digital-imaging methods) and requires little expensive equipment — just a camera and usually a tripod. Additional lighting can help to highlight morphological features, and most museum collections have a photography stand. The background of the image is often important, particularly when it is necessary to see the boundary of the specimen clearly. One way of creating a non-reflective dark background is by placing a piece of black velvet under the specimen. The angle of the specimen relative to the camera lens is also important if the goal is to make meaningful comparisons of the shape of several specimens. The angle can be altered using modelling clay or wedges of foam plastic to support the object.

Photogrammetry: Within the last few years, a method has been developed for creating three-dimensional (3D) images by taking multiple photographs of an object from various angles. As long as the photographs overlap enough, so that each pixel of the image has been registered from at least three different views, software can combine these photos using triangulation methods (using the focal length and depth of field of the image) to transform the 2D pixel information from individual photographs into a 3D virtual model.

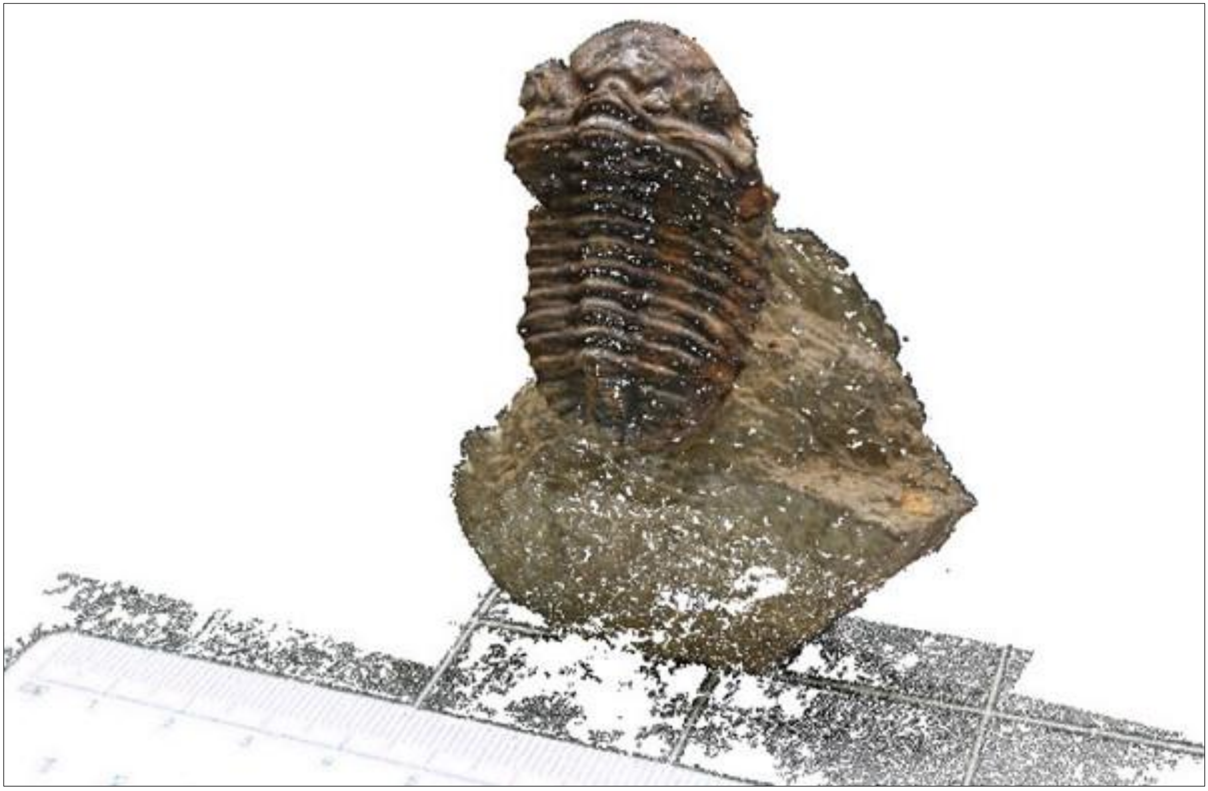

FIGURE 2 — A 3D IMAGE OF A TRILOBITE FOSSIL, IMAGED USING PHOTOGRAMMETRY (SOURCE: FALKINGHAM 2012)

Microscribing: The microscribe is an articulated arm ending in a point, or stylus, attached to a heavy base. 3DCartesian coordinates (distances along the x, y and — in the case of 3D data — z axes) are recorded by placing the stylus on chosen points of a shape and pressing the foot pedal to register the coordinates in a text file or spreadsheet. It is important that the object is kept still during this process to avoid mistakes. This tool is most frequently used to collect shape data in geometric morphometric studies, which simplify the shape to a configuration of landmark points (see ‘Statistical comparison of shapes’, below).

FIGURE 3 — A MICROSCRIBE (LEFT) AND LASER SCANNER (RIGHT).

Laser scanner: Portable laser scanners can be used to capture surface morphology of biological objects. They create point clouds of the surface topology of an object. Usually the specimen being imaged is rotated on a stage in front of the scanner, allowing it to capture the surface from different angles — although this doesn’t work with the largest samples. A complete image is achieved by compiling these views. The scanner may also be equipped with a camera that takes a photograph with each rotation of the object. This image is then laid over the model created from the laser to create realistic colouring in three dimensions.

CT scanning: CT scans are created using a combination of many X-ray images. If an X-ray has passed through a dense substance, the signal will be weaker than if it has passed through one which is less dense. This difference in X-ray strength is detected by a sensor behind the object and used to create an image. The X-ray beam and detector in a CT scanner both move in a circle around the object as the X-ray images are collected, unlike in standard X-ray images, for which they remain in a fixed position. The views from different angles can be used to create a cross-sectional ‘slice’ through the object. Many of these slices are then combined through digital processing to form a 3D images. CT scanners are most frequently used to look at internal morphology, because they create volume images based on differing densities of the material being scanned. These are composed of 3D pixels, known as voxels. This method is by far the most data-intensive in terms of the size of image file produced.

FIGURE 4 — A CT SCAN OF THE SKULL OF A DINOSAUR (EORAPTOR, SOURCE). SCALE BAR 1CM.

Before digital imaging, 3D fossils that could not be removed from their surrounding rock matrix were investigated by physically cutting the specimen into multiple slices to produce a ‘book’ of cross-sections from which morphology could be studied. Software specifically designed for transforming this cross-sectional information into a 3D image has been developed, and can also be used to process CT data. The benefit of CT imaging, however, is that it can produce 3D images of fossils enclosed in matrix without destroying the specimens — as long as there is a difference between the density of the fossil and the density of its surrounding matrix. CT scanning is also far less time-consuming than sectioning.

CT scans are often used as the geometric model when performing a technique called finite element analysis (FEA), which takes a complex shape and divides it into many smaller, simpler shapes to measure mechanical properties of the structure.

Statistical Comparison of Shapes:

Geometric morphometrics, a method for comparing complex biological structures, has gained much popularity in palaeontological research. It uses the Cartesian coordinates of ‘landmark’ points to describe a shape.

Choosing Landmarks: Landmarks fall into three categories according to how precise or homologous they are considered to be:

Type I landmarks: boundaries between tissues. In mammal skulls, for example, these can be suture junctions, where one bone touches another.
Type II landmarks: the peaks and troughs of curves, such as the outside edge of the eye socket or the frontmost point of the hole where the spine enters the skull.
Type III landmarks: the extreme end points of a biological structure, such as the very front and back of the skull.

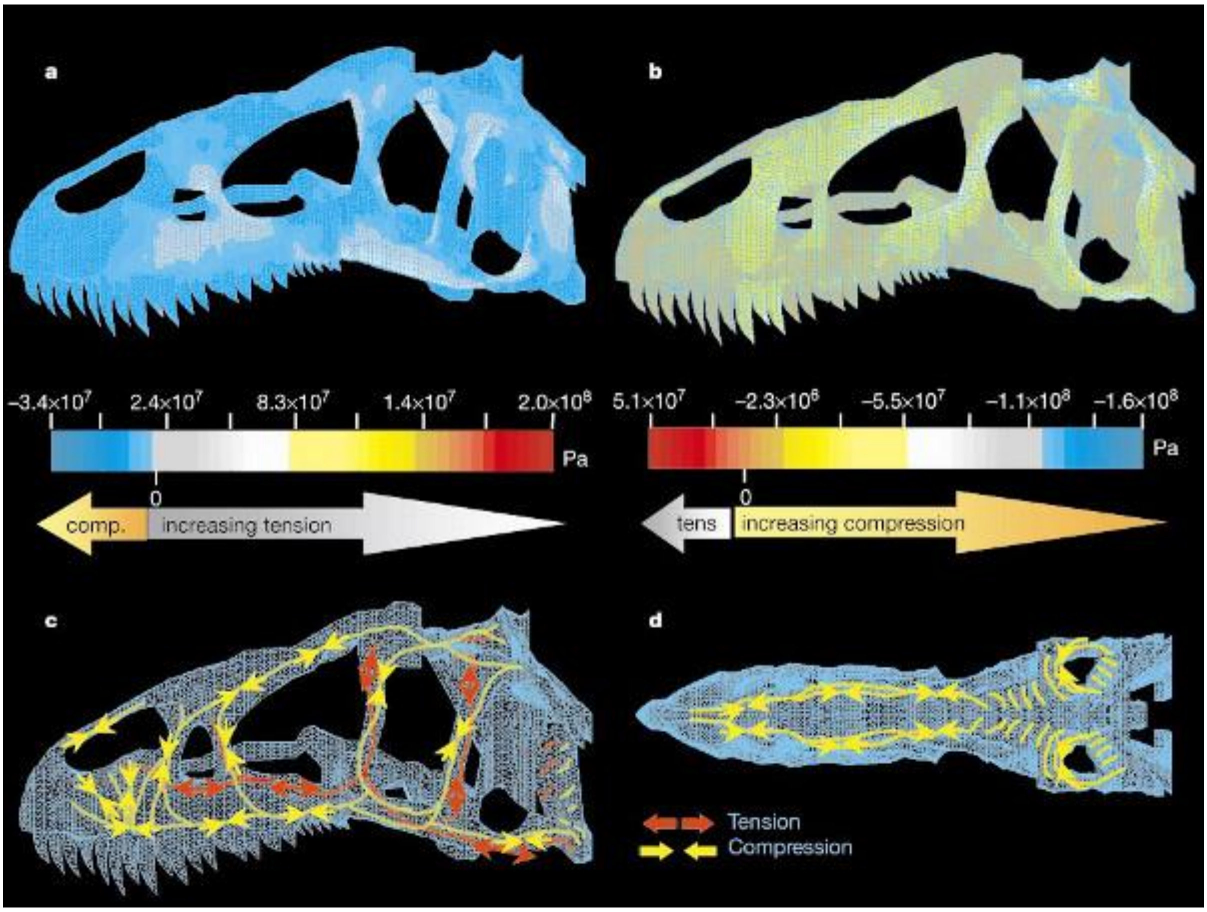

FIGURE 5 — FEA OF A DINOSAUR SKULL (ALLOSAURUS) MODELLING THE DISTRIBUTION OF STRESSES DURING BITING. SOURCE: RAYFIELD, E. J., NORMAN, D. B., HORNER, C. C., HORNER, J. R., SMITH, P. M., THOMASON, J. J. & UPCHURCH, P. 2001. CRANIAL DESIGN AND FUNCTION IN A LARGE THEROPOD DINOSAUR. NATURE 409, 1033–1037. DOI:10.1038/35059070

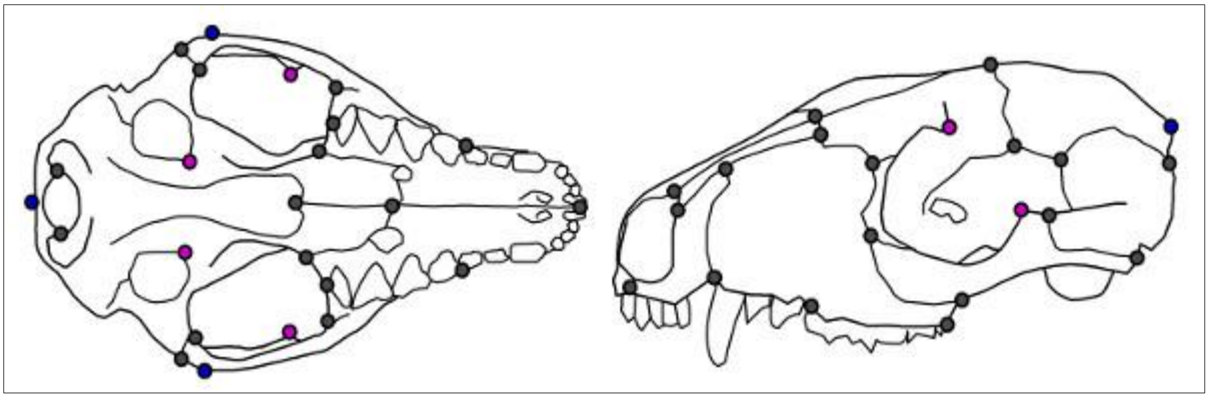

FIGURE 6 — DIFFERENT TYPES OF LANDMARKS ON A MAMMAL SKULL. GREY, TYPE I; PINK, TYPE II; BLUE, TYPE III.

Of these, type I landmarks are the most similar between life forms and can be placed with the most precision. However, the more distantly related two species are, the fewer truly homologous landmarks there are likely to be. The use of type II or III landmarks might be necessary to ensure full coverage of particular morphological features. How much landmarks correspond between specimens has phylogenetic, structural, developmental and biomechanical significance. But judging landmark correspondence is subjective and depends on the research question, as does the number and distribution of landmarks.

There are three major limitations with analysing the placement of landmarks one by one in specific locations. First, the whole form is not being described, so important, interesting and useful features that occur between landmarks — such as spaces, curves or other surfaces — can be overlooked. Second, the reliance on correspondence between the landmarks focuses on similarities, making large differences, such as the presence or absence of a feature, essentially impossible to capture. This potentially leads to an underestimation of variation. Third, some regions of the skull (with, for example, clear suture junctions or obvious peaks and troughs of curves) might be more suited to landmarking than others (such as large, smoothly curved surfaces) so some parts of the morphology can be overrepresented in comparison with others.

Other ways of describing shape have been developed, most notably the analysis of outlines and curves along which landmarks are evenly spaced. These are beyond the scope of this article, but more information can be found in the suggested reading.

Isolating shape data: Once landmark data have been collected from the biological sample, it is necessary to remove all size and position information, to leave only shape information. Several methods for doing so have been devised and argued for, but the most favoured method in literature from the last fifteen years has been Procrustes analysis. This gets its name from Procrustes, a morbid character of Greek mythology, known for inviting people to lie down in his bed, then adjusting them to fit into it, either by stretching them or cutting off their limbs. Procrustes analysis is the process of superimposing one collection of landmark configurations on another by scaling, rotating and translating them so that the distances between corresponding points in each configuration are as small as possible, making a 'consensus shape'.

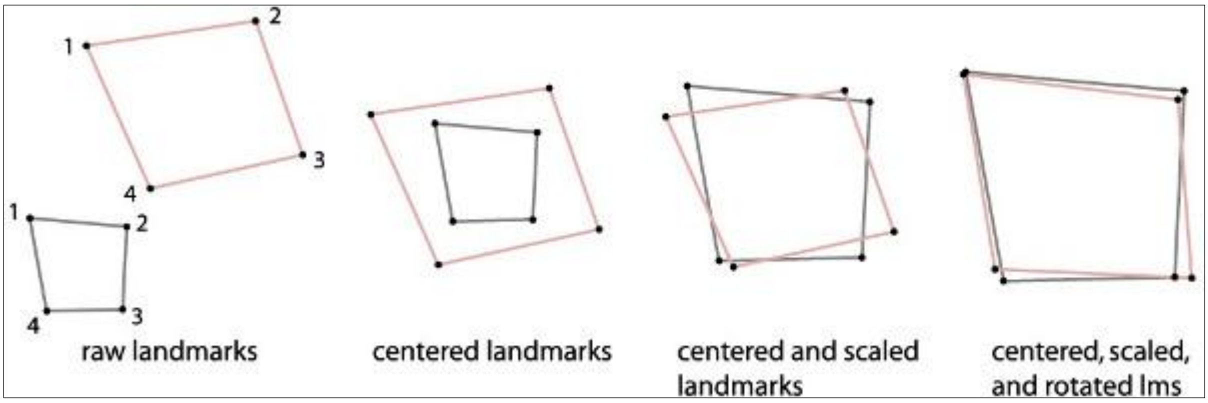

FIGURE 7 — DIAGRAM REPRESENTING THE DIFFERENT STAGES IN A PROCRUSTES SUPERIMPOSITION OF TWO SETS OF LANDMARKS. SOURCE: MITTEROECKER, P. & GUNZ, P. 2009. ADVANCES IN GEOMETRIC MORPHOMETRICS. EVOLUTIONARY BIOLOGY 36, 235–247. DOI:10.1007/S11692-009-9055-X

Analysing Shape: The new configurations of landmarks can be used to estimate standard statistical parameters. For example, the difference between any two shapes — their 'disparity' — can be calculated by finding the distance between the two sets of Procrustes landmark coordinates that represent those shapes. This is the Procrustes distance. Shape variance (the amount of variety in the shape data) can be calculated by adding together the squares of the distances between Procrustes landmarks and their equivalent landmarks on the consensus shape for all the landmark configurations in a sample. The total of the squared distances can then be divided by the number of configurations minus 1 to normalize it.

Often, when many specimens with many landmarks are being compared, the number of variables makes further interpretation of the results tricky, because multivariate space is impossible to visualize. Principal coordinates analysis (PCA) is a common statistical method that finds the major axes of variation through multivariate space. Figure 8 demonstrates PCA for just two variables (X1 and X2) for the sake of simplicity, but the idea is exactly the same when finding the principal coordinates (PCs) for data sets of many variables. Figure 8a shows the distribution of data points according to their X1 and X2 values, and Fig. 8b is a simplification of the shape of this distribution. PCA finds the axes of maximum variation through the data: PC1 is the longest axis and PC2 the second longest, at right angles to PC1 (Fig. 8c). The more variables there are in the data set, the more PCs there can be. Figure 8d shows how the original data is rotated to show variation according to the major axes of variation.

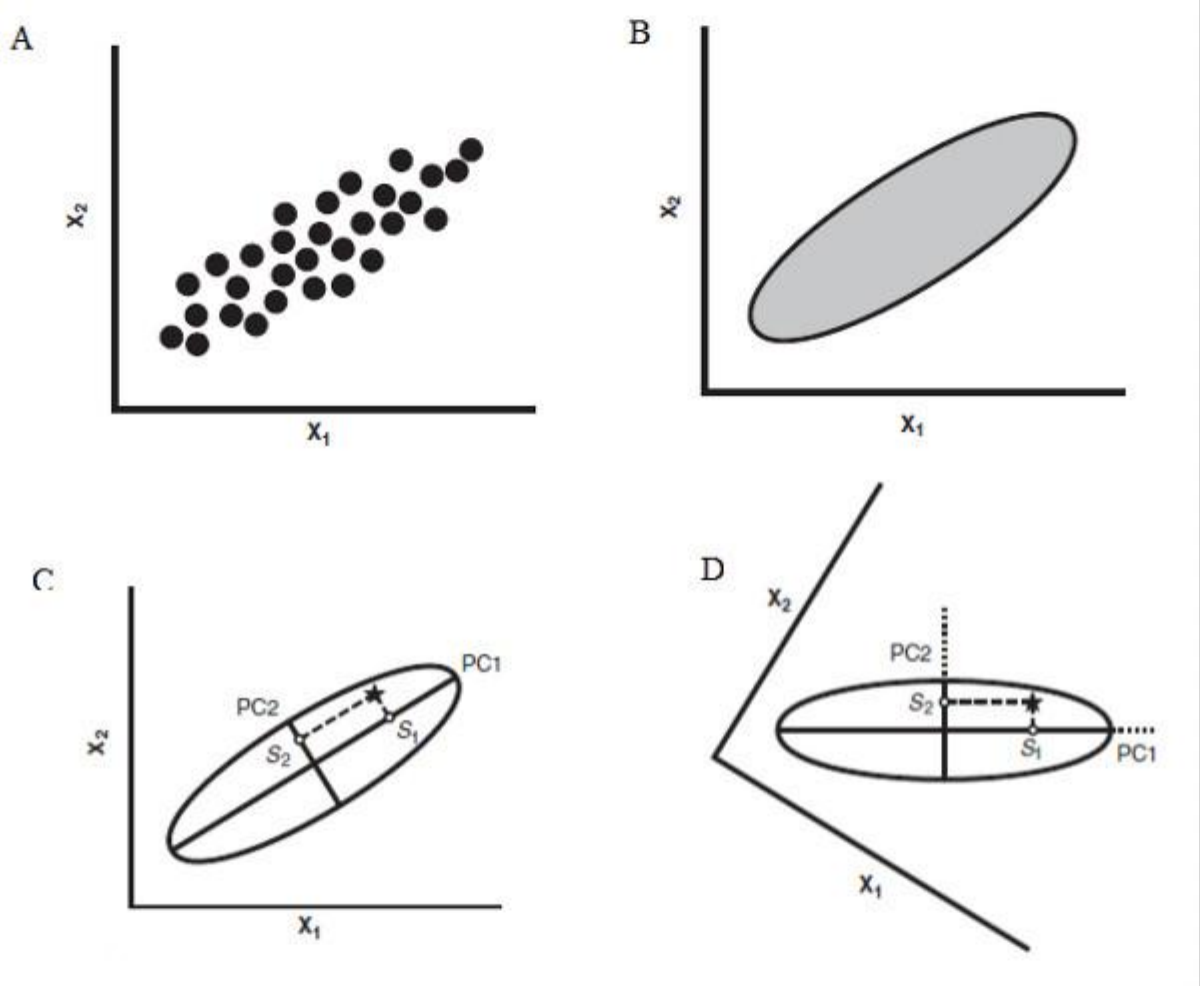

FIGURE 8 — A SIMPLIFIED GRAPHICAL REPRESENTATION OF WHAT PCA DOES TO DATA. REARRANGED FROM: ZELDITCH, M. L., SWIDERSKI, D. L., SHEETS, H. D. & FINK, W. L. 2004. GEOMETRIC MORPHOMETRICS FOR BIOLOGISTS: A PRIMER. ELSEVIER ACADEMIC PRESS.

Geometric morphometric data can be visually simplified by plotting the specimens against the PCs that explain the most variation in the data set. The area of this graph represents shape space, and the points are particular shapes within that space. In Fig. 9, the shapes are skulls.

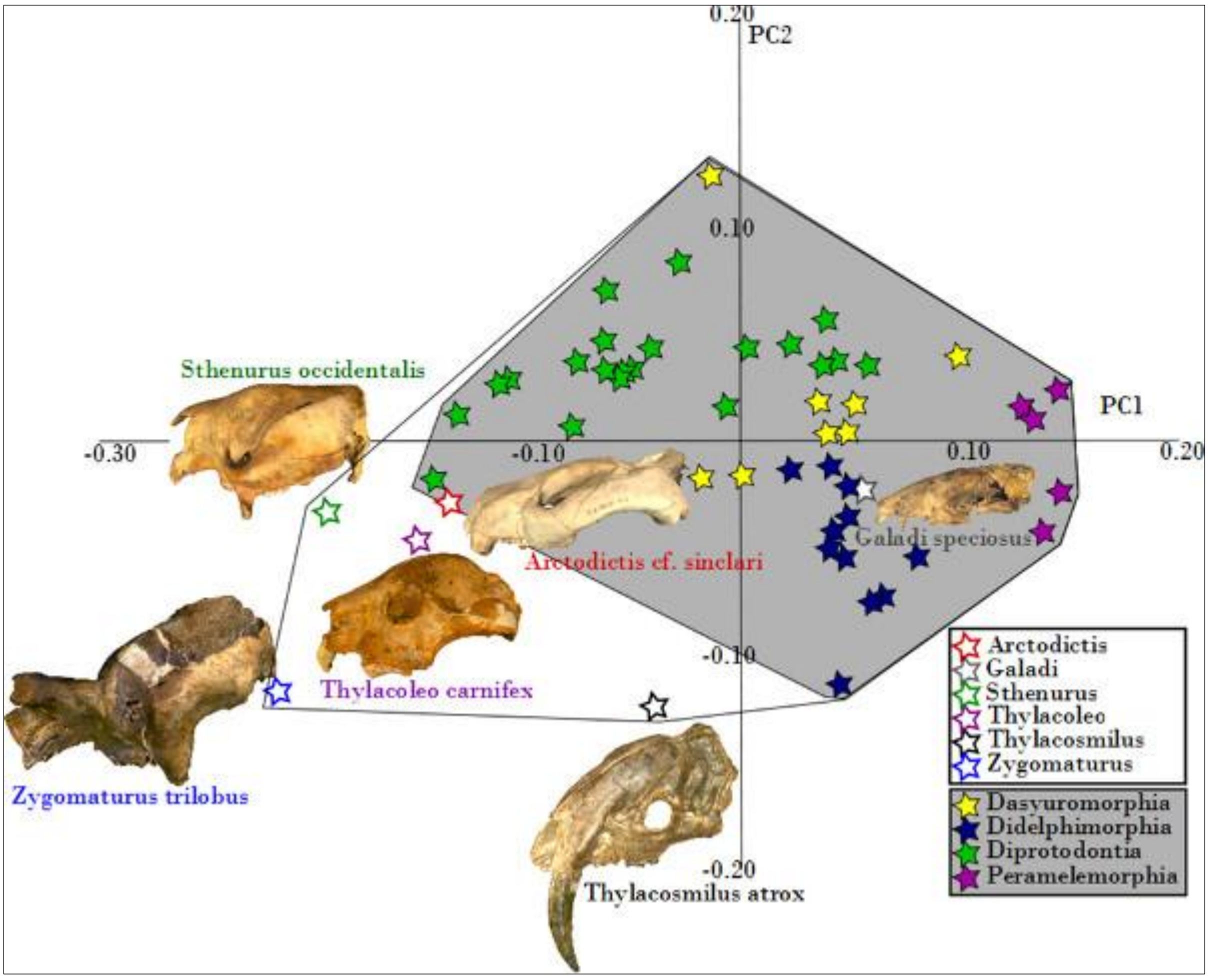

FIGURE 9 — PRINCIPAL COMPONENTS ANALYSIS OF EXTANT AND EXTINCT METATHERIAN SKULLS.

Summary:

This article is a short summary of the big and exciting world of shape analysis — much more detailed descriptions of imaging and analysis techniques can be found in the suggested reading. The shape of fossils is central to a wide range of palaeontological studies, and there are many ways of collecting and analysing such data, as shown in this article. However, each method has particular limitations that need to be weighed up, including cost, resolution, computing power, destructiveness, portability and amount of data. Choosing the most appropriate method depends heavily on the research question, the available funds (many of these techniques require expensive equipment or software) and the nature of the fossils. Palaeontological research has come a long way from the descriptions written by the fossil hunters of yore, and although thorough qualitative descriptions of specimens are still an important part of the science, modern palaeontology calls much more on cutting-edge technology from the realms of mathematics, physics and computer science.

Suggestions for further reading:

Adams, D. C., Rohlf, F. J. & Slice, D. E. 2004. Geometric morphometrics : Ten years of progress following the ‘revolution’. ***Italian Journal of Zoology*** **71**, 5–16. doi:1080/11250000409356545

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Mitteroecker, P., & Gunz, P. 2009. Advances in Geometric Morphometrics. ***Evolutionary Biology*** **36**, 235–247.doi:10.1007/s11692-009-9055-x

Zelditch, M. L., Swiderski, D. L., Sheets, H. D. & Fink, W. L. 2004. ***Geometric morphometrics for biologists: a primer.*** Elsevier Academic Press.

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