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Research Article

Shape descriptors as ecometrics in dental ecology

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Abstract

The revolution in morphometrics over the last 20 years has largely been in shape analysis methods that explicitly encode shape. These methods, which include Fourier outline shape analysis, Procrustes-based geometric morphometrics and eigenshape analysis, can be termed "shape specifiers". Despite their tremendous power in comparisons of shape, they do not give information about more general characteristics of shape that may be useful in interpreting function or ecology of an organism. "Shape descriptors" are computational representations of shape that can summarise high-level characteristics, such as overall shape or complexity. This paper describes a number of shape descriptors that have been used to capture specific morphological features of mammal teeth. Many of these dental shape descriptors have been valuable as "ecometrics", characteristics of organisms that reflect a species' ecology and can be used to reconstruct past environments. Shape descriptors can relate to the gross morphology or to the microwear texture of the tooth surface, as each of these have different characteristics and information regarding function and ecology. While this review concentrates on shape descriptors for teeth, it is hoped that they will give inspiration and stimulation to use and discover additional descriptors for other morphological systems.

Introduction

Shape is a fundamental attribute of organisms. We can think of shape as all that is left once size, translation and rotation are removed (Kendall, 1984). While this may sound simple, the scientific study and quantification of shape has been fraught with difficulties, both theoretical and practical. In the past, analysis of shape was often carried out using ratios of linear measures, or by angles. By themselves these capture relatively limited information about the morphology of interest, and ratios often do not remove the effects of scaling as expected (Atchley et al., 1976). With the greater availability of computers in the second half of the 20th century, multivariate morphometrics became the tool of choice for the study of shape by using multivariate statistical methods such as principal component analysis (PCA) to summarise variation in a large number of linear measures (Blackith and Reyment, 1971; Dryden and Mardia, 1998). This approach is now called "traditional morphometrics" (Rohlf and Marcus, 1993).

Great leaps forward have been made in the statistical analysis of shape in the last few decades. In modern morphometric methods, the geometry of the object is captured as outlines, landmarks, semilandmarks, or a combination of these. The suite of methods includes Fourier outline shape analysis (Christopher and Waters, 1974; Haines and Crampton, 2000), eigenshape analysis (Lohmann, 1983; MacLeod, 1999; Figueirido et al., 2011), Procrustes-based geometric morphometrics (Rohlf and Marcus, 1993; Richtsmeier et al., 2002; Adams et al., 2004; Slice, 2007), spherical harmonics (Funkhouser et al., 2003; Shen et al., 2009), eigensurface analysis (Polly, 2008; MacLeod, 2008; Polly and MacLeod, 2008; Sievwright and MacLeod, 2012), 3D semilandmark methods (Wood, 2011) and geometric similarity based on conformational geometry and optimal mass transportation (Boyer et al., 2011). Geometric morphometrics and eigenshape analyses utilise Euclidean projections of Kendall's shape space (Kendall, 1977, 1989; Dryden and Mardia, 1998). The intention of all of these methods is to preserve the geometry of the object and explicitly compare shape among objects, and so the shape of the original form can be recovered through these methods, at least as it is represented by the outline or landmarks. I will describe all of the above methods as "shape specifiers" where the intention is to specifically represent or encode the shape.

Despite the tremendous power that comes with these new methods, most of them are limited in the range of shapes that can be compared. This is particularly the case for those based on landmarks, in part because they require the same number of landmarks on all objects. This means that they cannot compare very dissimilar objects, or objects of different classes or types. It is not trivial to represent major differences between objects, such as the appearance or disappearance of structures, as these require changes in the number of landmarks. These limitations can partially be overcome (Klingenberg, 2008; Oxnard and O'Higgins, 2009), but this remains a major challenge in statistical shape analysis.

The analysis and comparison of shape can go beyond the specification of its geometry. In comparing shapes, there may be high-level characteristics other than the specific shape itself that we would like to quantify and compare. The desire to compare apples with chairs has led to a broader suite of methods for comparing shape. Shape can be categorised or quantified using transformations that do not retain position information but instead capture aspects of shape. We can call these computational representations of shapes "shape descriptors" (Christopher and Waters, 1974; Funkhouser et al., 2003). They are statistics about the shape without trying to encode the shape itself.

Shape descriptors have been used in computer science to index shapes based on their statistical properties. These can be for either 2D images or 3D models; I will largely concentrate on 3D shape descriptors here. They have been used to aid 3D shape matching and

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searching and the automatic shaped-based retrieval of 3D models from large databases or web searches (Funkhouser et al., 2003).

3D shape descriptors used in computer science include moments of inertia (Elad et al., 2001), Extended Gaussian Image (EGI, a spherical function giving the distribution of surface normals; Horn 1984), spherical extent function (EXT; Saupe and Vrani 2001), shape histograms (histogram of how much surface resides at different radii from centre of mass; Ankerst et al. 1999), Light Field Descriptor (LFD, a representation of a model as a collection of images rendered from uniformly sampled positions on a view sphere; Chen et al. 2003), Depth Buffer Descriptor (DBD, a collection of depth buffer images captured from orthogonal parallel projections; Heczko et al. 2002) and D2 shape distributions (probability distributions of geometric properties computer for points randomly sampled on an object's surface; Osada et al. 2002). Spectral shape analysis based on Laplace-Beltrami spectra includes Shape-DNA (Reuter et al., 2005, 2006), Global Point Signature (GPS; Rustamov 2007) and Heat Kernel Signature (HKS; Sun et al. 2009). I mention only global shape descriptors here, which consider the shape as a whole; most recent search methods use local shape descriptors as well, which only refer to parts or elements of the shape. These types of methods are used in the annual Shape Retrieval Contest (SHREC), held since 2006, e.g. SHREC'12 (Li et al., 2012). The usefulness of these types of descriptions can be seen in the creation of MPEG-7 standards for 2D- and 3D-shape descriptors, which could enable searching of video for specific shapes. See van Kaick et al. (2011) for a recent review of the field.

Shape descriptors allow for holistic and higher-level measures of morphology, including overall shape and complexity. Unlike shape specifiers, the original shape usually cannot be reconstructed from the shape descriptors. Individual or groups of shape descriptors can be a form of bar-coding or fingerprinting, and can potentially be used for copyright protection of 3D models (Reuter et al., 2005). The main contrast between specifiers and descriptors is that the former is a representation of shape, while the latter is an abstraction. In investigating shape descriptors for biological morphology, it is likely that the criteria for useful or good shape descriptors will be very different to those used in computer science mentioned above. This will very much depend on the type of questions being addressed.

Dental ecology

A lot can be gleaned about a mammal just from its teeth. They are key to food acquisition and processing in most mammals, and their shape has substantial influence on their ability to carry out these functions. As well as being useful for taxonomic identification, often showing species-level variation, they are the most frequently preserved component in the fossil record. Steven Jay Gould, well-versed in teeth, once quipped that "mammalian evolution is a tale told by teeth mating to produce slightly altered descendant teeth" (Gould 1989: 60). Teeth are so important to our understanding of various aspects that the term "dental ecology" has been coined, referring to the study of how teeth respond to the environment (Cuozzo and Sauther, 2012). Analysis of tooth shape should therefore give information on food types that the species has adapted to consume, as well as the effect of wear over the lifetime of the animal.

Mammal teeth exhibit a surprising diversity of shapes (Ungar, 2010), which is both a blessing and a curse for shape analysis. The variability in number and position of cusps, crests and basins, as well as the effects of wear, mean that the use of homologous landmarks to specify the positions of these features on the surface is not possible when comparing a functionally and/or phylogenetically wide range of teeth. This led to the use of shape descriptors to quantify and compare tooth shapes, from the intraspecific (Zuccotti et al., 1998; Ungar and Williamson, 2000) to the order level (Evans et al., 2007b). Mammal teeth are now an important model system for investigating shape descriptors in biological morphology.

Certain characteristics of teeth increase the difficulty of assessing shape compared to other systems. During the life of a mammal, its teeth will generally wear and change shape in the process. The initially-erupted primary occlusal morphology, where the entire crown is covered in enamel, can be worn to produce a secondary occlusal morphology, resulting in a series of dentine basins surrounded by enamel. The resulting change in shape can have a significant effect on the function of the teeth, and means that assessment of morphology should consider the effect of wear.

Landmark-based geometric morphometrics has been applied to some questions of tooth morphology (e.g. Ungar et al. 1994; Hlusko 2002; Skinner et al. 2008; Piras et al. 2010; Singleton et al. 2011), but in all cases the comparisons are very limited phylogenetically and morphologically.

Ecometrics

Due to their functional importance, teeth often reflect critical characteristics of a species' ecology. Because of this, they can be used to interpret past climates given modern associations between characteristics and modern climates. Taxon-free functional trait analysis, or "ecometrics" (Eronen et al., 2010c; Polly et al., 2011), is the association of such characteristics with climate or environment. Ideally such traits are largely independent of taxonomy, such that they can be measured on a wide group of species within a larger taxonomic group. Ecometrics has been used to give a deep-time perspective on climate change using traits such as leaf shape (Wolfe, 1995), body size (Legendre, 1986) and mammal locomotion (Polly, 2010). Several aspects of tooth shape have or could be used as ecometrics.

Dental Shape Descriptors

As teeth are such a favourite of mammal palaeontologists, there has been a veritable explosion of proposed methods to quantify their shape. Here I briefly survey a range of shape descriptors that have been useful in functional interpretations of tooth shape, in comparative study across a broad taxonomic range, and as ecometrics for dietary and paleoenvironmental reconstruction.

These descriptors vary greatly in their ease of measurement, such that some can be measured using callipers while others need full 3D surface data. However, measurement simplicity is not necessarily related to their usefulness in functional or ecometric analysis. While simple shape descriptors such as hypsodonty capture very little information of the shape of the tooth, they are still powerful ecometrics.

Some of the shape descriptors here will be only applicable to teeth (e.g. shear ratio and mesowear), while others will be more generally applicable to a wide range of surfaces (e.g. OPC and microtexture analysis). One purpose of this review is to show the great variety of approaches for assessing shape in teeth; another is to show biologists working on other morphological systems the types of aspects that may be applicable to their work – to give inspiration for new ways of looking at morphology.

Gross topography

The chewing, or occlusal, surfaces of mammal teeth vary dramatically, from a few simple bumps to washboards to blades. These measures of topography intend to quantify aspects from overall form to the shape of specific regions of the teeth.

Ratios and Angles

Several simple measures have been extensively used to gauge overall tooth shape. Molar length-width ratios are common, particularly in physical anthropology, and can help in assigning a specimen to a taxon. Relative crown height, or hypsodonty, is measured as height:length or height:width ratios (Simpson, 1953; Van Valen, 1960; Janis, 1988; Fortelius et al., 2002; Damuth and Janis, 2011), and is an important ecometric correlated with precipitation (Fortelius et al., 2002; Eronen et al., 2010a,b; Liu et al., 2012; Raia et al., 2011). In carnivores, carnassial tooth shape has been quantified by the angle α, which relates the height of the protoconid relative to the length of the talonid (Crusafont-Pairó and Truyols-Santonja, 1956). This character is indicative of the level of carnivory (Wesley-Hunt, 2005) and can reveal the evolution of trophic position in carnivores (Meloro and Raia, 2010).

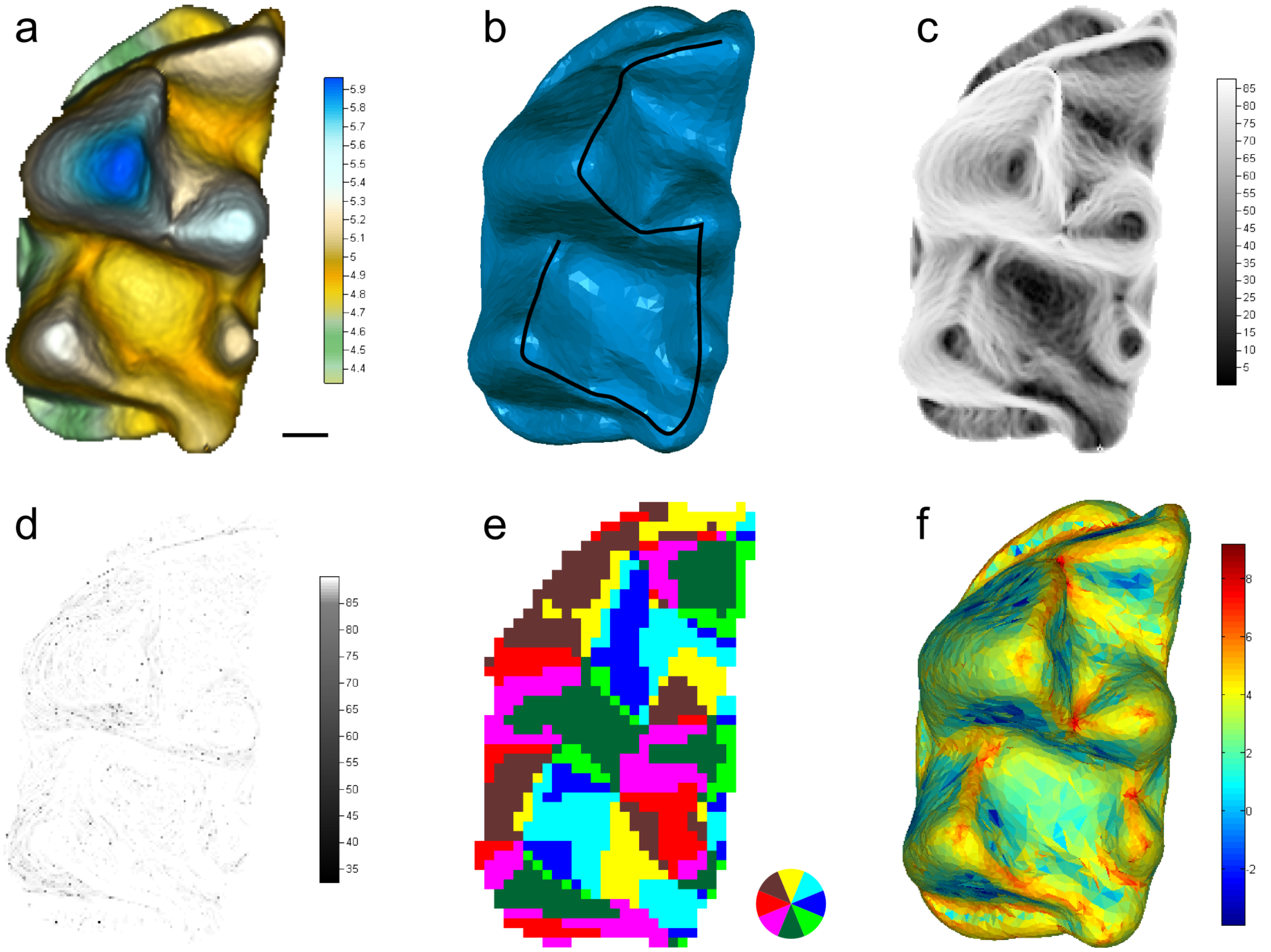

Figure 1 – Comparison of a number of gross morphology shape descriptors outlined in this review, illustrated using the dasyurid marsupial *Antechinus agilis* NMV C12676 (Museum Victoria) left lower second molar in occlusal view. a) Height-encoded map (height in mm); b) shearing edges measured for calculation of shear ratio; c) slope (in degrees); d) angularity (in degrees); e) aspect map for OPC calculation (colour wheel shows orientation); f) Dirichlet normal energy. Mean slope: 55.94; mean angularity: 89.720; Relief index 2D (M'Kirera and Ungar, 2003): 2.75; Relief index 3D (Boyer, 2008): 0.66; OPCR: 50.25; DNE: 508.39. Number of surface points: 18853 (c), 18326 (d), 980 (e) and 9995 (f). Number of anterior-posterior data rows: 50 (e). Illustrations made using Surfer (a, c, d), Geomagic (b), Surfer Manipulator (e) and Teether (f). Scale bar = 0.2 mm.

While ratios can reveal some aspects of morphology, they give no information on the outline or topography of the tooth. More specific measures of the shape of tooth components can reveal relative function of cusps and crests (Evans and Sanson, 1998, 2003). Rake angle, approach angle and edge sharpness are key shape descriptors for crest function that describe the orientation of the cutting edge and its surrounding surface relative to the direction of movement (Evans and Sanson, 2003, 2005). Changes in these factors will affect the performance of the teeth for fracturing viscoelastic foods, and can therefore quantify relative performance in unworn and worn teeth.

Shear Ratio

Kay (1975, 1978) developed one of the earliest shape descriptors for dental topography that is useful in assessing diet and ecology of primates. "Shearing quotient" and "shearing ratio" measure the relative lengths of shearing crests on the surface of a tooth (e.g. Fig. 1b). They have been extensively used in interpreting diets of placentals (see Bunn et al. 2011 for review) and marsupials (Hogue and ZiaShakeri, 2010). Disadvantages of shear ratio include the requirement of specifying the crests to measure, and its inability to deal with variable wear states (Evans and Sanson, 1998).

Mesowear

Wear on teeth during the lifetime of an animal often has a substantial effect on their shape. In many instances this has a detrimental effect on the function of the teeth (Evans, 2005; King et al., 2005). But the way in which tooth shape changes during the wear sequence is greatly influenced by the relative amounts of attrition (tooth-tooth) and abrasion (tooth-food) wear. The former tends to produce planar facets with sharp edges, while the latter causes rounding of tooth surfaces. This difference has been useful when examining wear in animals with secondary occlusal morphology, such as artiodactyls and perissodactyls, where the functional surface results from and is maintained by wear (Fortelius, 1985). If attrition dominates, as it tends to do in browsers, the resulting crests are sharp with high relief, while with increasing amounts of abrasion, found in grazers, relief is lower and the crests are rounded. With sufficient sample size for a species or population, this signature of mesowear shows a good association with dietary classification (Fortelius and Solounias, 2000).

Kaiser et al. (2013) comprehensively reviewed the associations between hypsodonty and mesowear. They found that mesowear largely indicates diet (percentage of grass in natural diet), while hypsodonty also includes effects from the environment (mean annual precipitation and openness of habitat) as well as diet.

Crown Types

To enable a broad-scale morphological comparison of teeth, Jernvall (1995; Jernvall et al. 1996) developed a topological system for categorising dental shape called "crown types". The crown type is a four-digit code counting the number of buccal and lingual cusps, and the number of longitudinal and transverse lophs. A significant feature of this method is that it assessed both developmental and functional aspects of shape, as cusps result from the folding during development of the mesenchyme-epithelium interface.

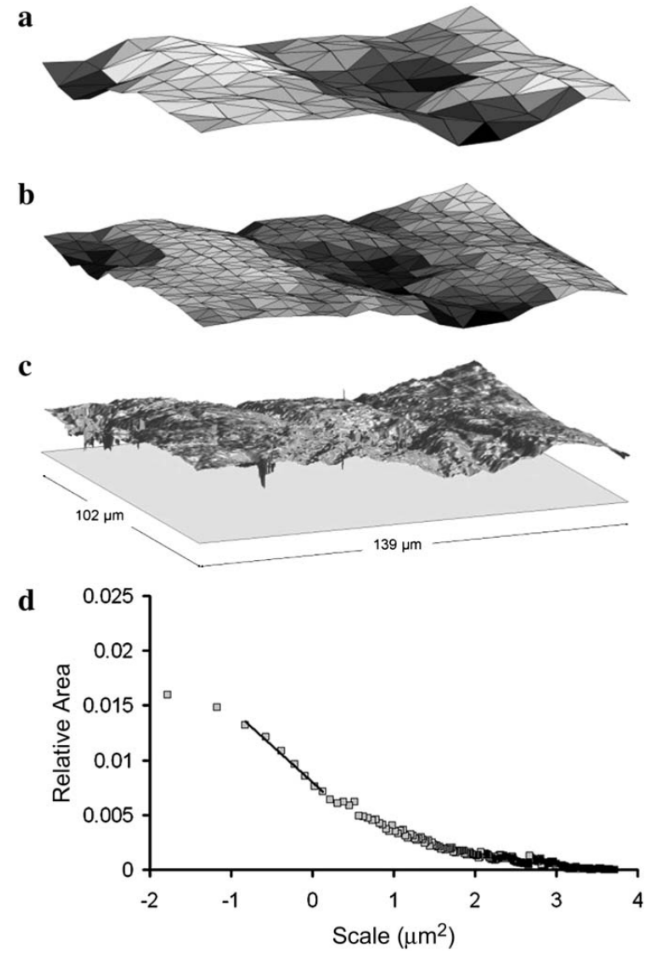

Figure 2 – Area-scale analysis in SSFA. A virtual tiling algorithm using triangles of different sizes can be used to measure surface roughness (compare a, b, and c). Complexity is represented by the steepest part of a curve fitted to the plot of relative area over scale (d). From Scott et al. (2006).

Jernvall et al. (1996) used crown types to show the difference between the Eocene and Miocene radiations in ungulate communities, with the former having higher diversity in tooth shape but lower disparity, while the latter displayed an increase in the number of lophs to presumably deal with lower quality vegetation. Together with hypsodonty, the number of longitudinal lophs highly correlates with net primary productivity (Liu et al., 2012).

Relief Index

Real-world objects are always a three-dimensional volume surrounded on all sides by a surface. However, the functional surface of teeth can largely be viewed from a single direction, as in a photograph. This type of projection of a 3D surface onto a 2D plane we can call a 2.5D surface, where for every position on an xy grid there is only one surface, at height z. Undercuts, where one part of the surface curves underneath another part, cannot be represented in 2.5D. As the crown of the tooth passes into the gingiva, the tooth tapers underneath the crown into the root or roots. However, the majority of the crown above the cervical region can be represented by 2.5D. There are many advantages to this simpler representation. Computation of surface characteristics is much simpler, including Geographic Information Systems (GIS) algorithms, which are often based on raster (gridded) 2.5D data. The use of GIS and tooth digital elevation models (DEMs) began in the late 1990s (Reed, 1997; Hunter and Jernvall, 1998; Zuccotti et al., 1998; Jernvall and Selänne, 1999; Evans et al., 2001) and has been termed "dental topographic analysis" (Ungar and Williamson, 2000).

A number of measures were first developed by Ungar and Williamson (2000) to describe shape. Relief index is the ratio of the 3D surface of a tooth to its projected 2D area. In the initial formulations, 3D surface was calculated for a 2.5D crown surface, which may only extend down the sides of the tooth to the same level as the bottom of the lowest basin (Ungar and Williamson, 2000). However, it is also possible to measure 3D surface for the full crown of the tooth (Boyer, 2008; Bunn et al., 2011). Relief index is usually considered to measure overall height of the crown or component cusps, but there is the potential for height and complexity to be confounded in the measurement of relief index (Plyusnin et al., 2008). Tooth wear reduces relief index in most species, as the height of cusps is worn down, and so wear state should be taken into account when examining relief index.

M'Kirera and Ungar (2003) calculated relief index as SA/PA, where SA is 3D surface area and PA is 2D planar area. Boyer (2008) measured relief index as $\ln\left(\sqrt{SA}/\sqrt{PA}\right)$.

Relief index has been shown to differentiate diets in primates (Boyer et al., 2010; Godfrey et al., 2012; Bunn et al., 2011). Ulhaas et al. (2004, 2007), Dennis et al. (2004) and Klukkert et al. (2012) also use relief index to assess differences in relief among species and with wear.

Average Slope and Angularity

The slope can be measured at each point on a surface using GIS algorithms (Fig. 1c). An overall measure of tooth shape can be made using the average slope (Ungar and Williamson, 2000; M'Kirera and Ungar, 2003; Klukkert et al., 2012).

Angularity is the average rate of change of surface slope, calculated as the slope of the slope map (Ungar and Williamson, 2000), and so is a measure of sharpness of the edges (Fig. 1d). Despite changes in slope following wear, angularity is seemingly robust to wear (Ungar and M'Kirera, 2003).

Orientation Patch Count (OPC)

GIS can also be used to calculate the orientation or aspect of the surface at all grid points of a 2.5D surface, either as an angle from a fixed direction (e.g. y-axis or north), or as cardinal and ordinal directions (e.g. north, south-west; Fig. 1e). Adjacent grid points that are facing the same direction can be grouped together using GIS clumping procedures into a "patch". The number of these patches over the surface gives the "orientation patch count" or OPC (Evans et al., 2007b). To account for differences in size and scanning resolutions, all specimens within an analysis are standardised to a given grid length, such as 150 grid rows for a tooth row, or 50 grid rows per tooth. The effect of the positioning of the tooth on the grid can also be mitigated by rotating the orientation boundaries and recalculating OPC. The resulting value can be termed OPCR (Wilson et al., 2012).

This method was designed to give an automated quantification of dental complexity along the lines of crown typing by removing the subjective classification of which cusps or features should be counted. For many tooth forms, OPC measurement is robust to wear (Evans et al., 2007a), likely indicating a maintenance of function throughout much of the wear sequence.

Dental complexity has been used in carnivorans, rodents (Evans et al., 2007b), primates (Boyer et al., 2010; Godfrey et al., 2012; Bunn et al., 2011), bats (Santana et al., 2011), multituberculates (Wilson et al., 2012), dasyurids (Smits and Evans, 2012) and in developing teeth (Harjunmaa et al., 2012).

Section Area and Convolution

The topography of the tooth can be quantified by examining the relative area and degree of folding of contour lines in the xy plane (Plyusnin et al., 2008). The tooth is sectioned 10 times in the xy plane, and the area and perimeter of the resulting cut surface are calculated. The area measurements are standardised by the total xy area, and convolution is the length of the perimeter of all parts of the section divided by the square root of the area of that section. Convolution measures the perimeter:area ratio and quantifies the degree of folding in the shape, such that it increases as the contour is increasingly folded. Both area and convolution can be used to give a profile of the shape of the tooth from crown to base, or each section can be used separately as a shape descriptor.

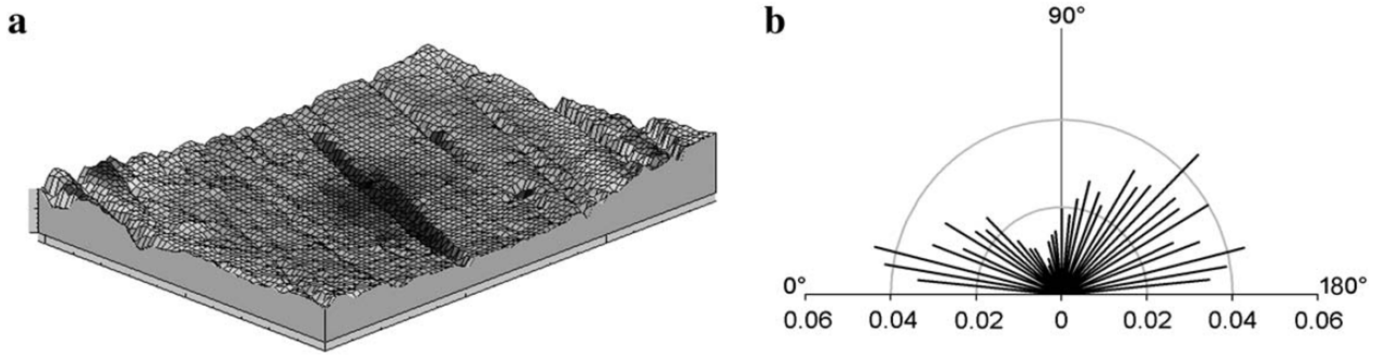

Figure 3 – Three-dimensional rendering of a striated surface (a) and the corresponding rosette plot of relative lengths taken at 36 different orientations (b). From Scott et al. (2006).

D2dist

Osada et al. (2002) conceived the descriptor D2, which measures the distance between two randomly chosen points on the surface of a model. The distribution of D2 distances was shown to be effective to distinguish a wide range of object classes. The descriptor was modified as D2dist by Plyusnin et al. (2008) for 2.5D surfaces such that the two points are chosen at random with respect to the xy plane. Plyusnin et al. (2008) used the mean and standard deviation of D2dist as shape descriptors.

Dirichlet normal energy (DNE)

Dirichlet normal energy was first used in dental topographic analysis by Bunn et al. (2011). It is based on the Dirichlet energy of the normal map of a surface, and quantifies the deviation of a surface from a plane (Fig. 1f). As a continuous function it is equivalent to measuring the sum of squares of the principal curvatures over the surface.

DNE has the advantages of being independent of position, orientation and scale. It gives an overall measure of curvature at crests and flatness of faces. Higher DNE may be the result of taller tooth features (giving larger flat faces), and is highly correlated with relief index. It reflects a change in both the height and the curvature of cusps/crests.

Microwear Surface

Surface shape extends in scale down to nanometre-level variations in surface height. Activities such as food acquisition, processing and grooming create fine use-wear features on the tooth surface called microwear. Analysis of microwear began in the late 1970s (Walker et al., 1978; Rensberger, 1978; Teaford, 1988), and showed that it was useful in distinguishing diet and/or environment. Until around 10 years ago, microwear analysis was largely been carried out by assessing the relative density and size of wear features such as pits and scratches from 2D SEM micrographs or light microscopy. Although Boyde and Fortelius (1991) suggested the use of 3D methods to examine microwear surfaces, 3D quantification did not commence until Ungar et al. (2003; Scott et al. 2006), who termed it dental microwear texture analysis. The two main sets of topographical measures have been used are described below.

Scale-sensitive fractal analysis

The initial methods to quantify dental microwear were based on scale-sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2005). SSFA relies on the fractal geometry of natural objects, where the measurement of quantities such as length and area depend on the scale of measurement (Mandelbrot, 1967). Several variables have been defined that quantify different aspects of this relationship (Scott et al., 2006).

A surface can be represented by large or small triangles, giving the "scale" at which the surface is measured. When the area of a surface is measured at increasingly small scales, the measured surface area increases as smaller and smaller features are included in the measurement. Area-scale fractal complexity (Asfc) measures the steepest section of a log-log plot of scale vs. measured area (Fig. 2). The scale at which this steepest relationship occurs is called the scale of maximum complexity (Smc). Heterogeneity of the surface can be quantified by measuring Asfc for varying subregions of the surface and calculating the relative variation from the median (HAsfc).

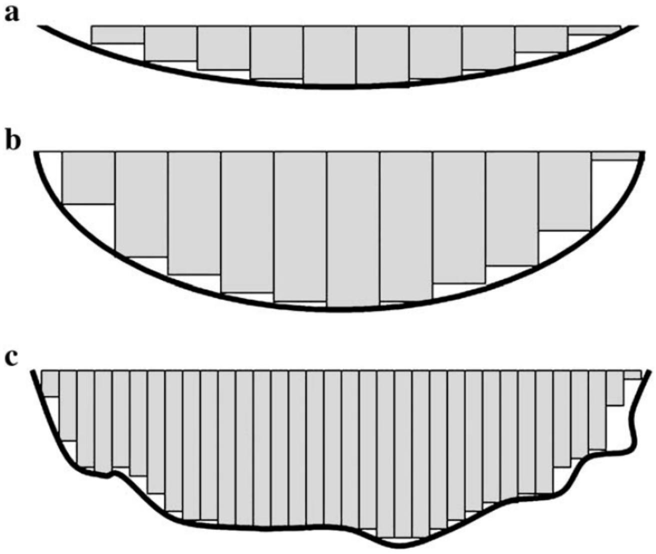

Figure 4 – Schematic comparing surfaces with (a) lower and (b) higher structural fill volumes. Finer scale prisms (c) yield structural and textural fill volumes. Textural fill volume is calculated by subtracting (b) from (c). From Scott et al. (2006).

The texture of a surface can have directionality, such as scratches in one direction. Profiles taken across the surface will vary in their length depending on whether the profile runs parallel to these scratches (and so will be flat) or perpendicular (and so will be zig-zagged). The normalized or "exact proportion" of the relative lengths can be used in a rosette diagram to visualise the degree of anisotropy (Fig. 3), and the mean vector length is defined as the exact proportion length-scale anisotropy of relief (epLsar). A higher value indicates that more wear features are perpendicular to that direction.

Variation in surface shape can also be measured by filling the volume with square cuboids of different sizes (Fig. 4). The general shape of the surface can be captured by larger cuboids, with a base length of 10 μm, measured as structural fill volume (Sfv). Using smaller cuboids (2 μm base length) will fill the finer texture of the surface, and is called the texture fill volume (Tfv).

There has been an explosion of papers using SSFA in the last three years, particularly on primates (Scott et al., 2009; Calandra et al., 2012; Merceron et al., 2009; Pontzer et al., 2011; Scott et al., 2012; Ungar et al., 2012a). SSFA has been used in other groups ranging from, bovids (Scott, 2012), cervids (Merceron et al., 2010), tragulids (Ungar et al., 2012b), macropodids (Prideaux et al., 2009) and carnivorans (Schubert et al., 2010; Stynder et al., 2012).

ISO surface texture parameters

Dental surface texture has also been investigated using two different ISO standards. The first set, from ISO 4287 (1997), quantifies roughness based on 2D surface profiles. It includes variables such as maximum (Rp), minimum (Rv), roughness average (arithmetic mean deviation; Ra), fractal dimension (Rfd), asymmetry (Rsk), kurtosis (Ruk), density of peaks (RHSC), and root mean square deviation (Rq) of each profile. Kaiser and Wolff (2005) were able to distinguish folivorous primates from gramnivores based on subsets of these variables, and Kaiser and Brinkmann (2006) found a separation of grazers and browsers in bovids.

The second is a collection of standards for the measurement of 3D surface texture (ISO 25178-2 2007). These relate to aspects such as statistics of the height of the surface (maximum Sz, skewness Ssk, kurtosis Sku), the bearing area curve (cumulative probability density function; e.g. volume Vmp, Vmc), spatial parameters such as autocorrelation (Sal) and texture aspect ratio (Str) and direction (Std, Stdi).

Schulz et al. (2010) and Calandra et al. (2012) compared the ISO standards with SSFA, illustrating that the general results concur between the two methods, and they are able to distinguish diets of differing properties. Purnell et al. (2012) were able to use the ISO standards to discriminate diets in cichlid fish.

Software

Much of the software for measuring the 3D shape descriptors discussed here was written by the researchers for the explicit purpose of quantifying dental morphology, while the remaining is commercial software that carries out some or all required functions. Once a surface has been digitised (gross morphology by computed tomography (CT), laser surface or structured light scanning; microwear surfaces by confocal microscopy or interferometry), file format conversions are usually required from the raw data (which may be as point clouds or polygons) to a format accepted by the analysis software.

Lengths, angles, 2D and 3D areas and volumes (to calculate descriptors such as relief index) can be measured from polygon models using commercial software such as Geomagic (Geomagic USA, Morrisville, NC, USA), RapidForm (3D Systems Corp., Rock Hill, SC, USA), PolyWorks (InnovMetric Software Inc., Quebec, QC, Canada) and SolidWorks (Dassault Systèmes SolidWorks Corp., Waltham, MA, USA). Some measurements can be made using the open source software Meshlab (http://meshlab.sourceforge.net). Avizo and Amira (Visualization Sciences Group, Burlington, MA, USA) can calculate these measurements from CT data (e.g. image stacks). GIS software appropriate for some shape descriptors includes Surfer (Golden Software, Inc., Golden, CO, USA) and ArcView (ESRI Corp., Redlands, CA, USA). Surfer Manipulator is custom Visual Basic software for OPC analysis that integrates with Surfer (http://users.monash.edu.au/~arevans/software.html). ToothKit is Java software to calculate descriptors such as section area, convolution and D2dist (http://www.biocenter.helsinki.fi/bi/evodevo/toothkit/index.shtml). Teether is a MATLAB package for calculating DNE (available from Julia Winchester julia.m.winchester@gmail.com). SSFA is carried out using Toothfrax and Sfrax software (Surfract Corp.). The ISO 25178-2 2007 surface standards can be measured by the software accompanying the 3D scanner, such as µsoft analysis premium software (NanoFocus AG, Oberhausen, Germany; a derivative of Mountains Analysis software by Digital Surf, Besançon, France) and Alicona IFM software (Alicona UK Ltd, Kent, UK).

Discussion

For the large number of shape descriptors covered above, several have shown great usefulness as ecometrics in mammalian biology. In terms of gross morphology, those most currently in use are relief index and dental complexity, but it is likely that new descriptors such as Dirichlet normal energy will be more broadly applied in the near future.

As a method for quantifying morphology, shape descriptors will find a much broader use in biology and palaeontology, ranging from phylogenetics, population-level variation and correlation with genetic and developmental architecture. This is due to their flexibility in being able to represent a very wide range of morphologies, and so being able to compare within and even among disparate systems. The challenge of applying these types of techniques in the future will be to ensure that any descriptors or application of them keeps in mind relevance to a biological question or hypothesis.

One recent example of the application of dental ecometrics is that of Wilson et al. (2012) in exploring the patterns of evolutionary and ecological change in the Multituberculata. The multituberculates were the most diverse and long-lived Mesozoic mammals, ranging in body mass from about 6 g to 20 kg. Because there are no modern members of the group, it has been difficult to find an appropriate analogue to assess their palaeoecology. Using OPC as a measure of dental complexity, Wilson et al. (2012) were able to show that early multituberculates were carnivorous or omnivorous in their dietary habits, but underwent an adaptive radiation around 85 million years ago into a herbivorous niche. This was corroborated by an increase in body mass, likely to be advantageous in plant feeding, and coincided with the ecological rise of angiosperms. The shape descriptor of dental complexity provided a scale- and phylogeny-independent measure of trophic position that revealed the broad-scale evolutionary patterns in this important group of mammals.

At the moment there is no overlap in the shape descriptors applied to gross morphology and microwear surfaces. There are fundamental differences between these two: the former tend to have higher relief and fewer features, while the latter are often highly repetitive and vary over the entire tooth surface. It is therefore not surprising that different sets of shape descriptors have been useful for each. The shape descriptors for gross topology are largely not applicable to microsurface textures due to much lower relief and larger number of features in the latter. It is interesting to consider, however, the degree of variability in the two types of surfaces depending on the wear state of the tooth, and to what degree the various shape descriptors are insensitive or robust to it. Depending on the application, either of these may be required.

Another feature of surface microwear is that it is an acquired "morphology" as opposed to the primary morphology resulting from folding of the mesenchyme-epithelium interface and subsequent deposition of an enamel layer. Once wear has commenced, gross topology can also be primary-derived (Evans et al., 2005) or secondary (Fortelius, 1985). Genetic determination of these morphologies therefore varies from full (primary morphology), partial (worn gross morphology, as illustrated by mesowear signature and other patterns of differential wear, such as the different carnassial forms of canids and felids; Evans et al. 2005), or none (microwear). Each of these, therefore, gives different levels of ecometric information, from days or weeks (microwear), years (mesowear) to generations (gross morphology). Only through integration of these varying time scales will we have confidence in evolutionary and environmental signals we may detect.

Despite the name "shape descriptors", many do not strictly remove size in the same way as centroid size standardization used in Procrustes-based geometric morphometrics. Generally, size is controlled for in the topographic measures based on 3D surface data by the use of a fixed number of polygons or data rows to represent the surface (e.g. relief index, OPC). However, the ISO microwear texture variables are often absolute, giving measurements in micrometers so size has not been removed at all. Several of the SSFA variables also include some aspects of scale. In principle, fractal dimension should be independent of size, but biological surfaces are not self-similar at all scales and so the range of measurement lengths will influence the measurement of fractal dimension.

As well as those with already established usefulness as ecometrics, such as hypsodonty, OPC and SSFA, I anticipate that a number of others described above, or to yet be discovered, will give further insights into the evolution of mammalian morphology and ecology.

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