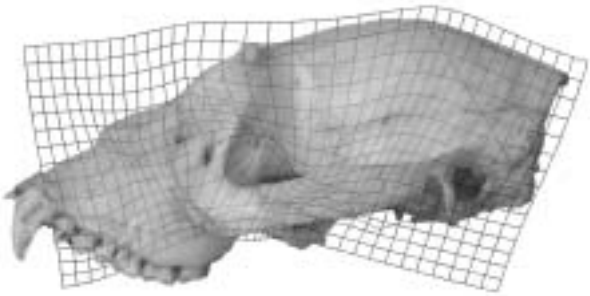
SHAPE MEETS FUNCTION: STRUCTURAL MODELS IN PRIMATOLOGY

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Models for Natural History

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Summary - *A model is a representation, a physical or conceptual object used to describe some qualities of another object. Therefore, a model only bears some properties of the object it represents, and is "true" only within the context in which it has been developed. Science is aimed at providing interpretations of reality; these are not good or bad, but merely more or less useful. In general, "model" is a rather heterogeneous and plastic term that needs to be defined and understood in every specific situation. Computed techniques have rapidly increased the analytical power of the morphological analyses. Such power can be controlled only by using an appropriate conceptual knowledge of these tools. The development of the computed tomographic facilities has improved the physical availability of specimens, structures, features, and variables. The morphology and the composition of the biological volumes are the qualities that have been integrated in the elaboration of the virtual image, with applications ranging from biomechanics to didactics. Geometric morphometrics probably represents the major recent contribution to the morphological approach. The high-resolution power is associated with the analysis of the structural and functional matrix of the biological forms, via the matching of landmark data with multivariate statistics. In this context, "model" is the configuration used to represent objects. However, model is also the multivariate shape space itself, generated by the correlations within the morphological network. It is possible to exploit the actual power of these resources only through the complete knowledge of these techniques' conceptual principles (requirements, constraints, and limits).*

Keywords - *Computed models, geometric morphometrics, computed tomography, digital morphology.*

Introduction

"*Newton did not shew the cause of the apple falling, but he shewed a similitude (the more to increase our wonder, with an apple) between the apple and the stars*"
(D'Arcy Wenthworth Thompson, 1942)

Computed analyses in evolutionary biology are relatively recent tools. Therefore, we are facing a set of new potentialities, which will lead to changes in the way we formulate questions, and interpret answers. Throughout the history of humankind, the awareness of the properties, potentialities, and limits of any important tool, has always followed its discovery and development. Consequently, there is a time gap (years, decades, or centuries) during which the new tool is managed badly, which leads to scarce results in comparison with its potentialities. Abuse and misunderstandings of the tool use can even lead to "damages", both directly through a misuse of its applications and culturally in supporting incorrect and dangerous paradigms. We are trying to promote what someone called the *in silico* approach, or the computed complement to the *in vivo* and *in vitro* experimentation. This introduction is aimed at creating a sort of framework for the current morphological computed techniques, trying to understand the role (more than the applications) of our digital tools. The scientific foundations of comparative anatomy and morphology can presently be improved by using some basic and well-known concepts of our his-

torical epistemology. The current use of computed models may represent and promote this chance (Bruner, 2003a).

The never-ending struggle between Science and Nature

Almost 2500 years ago Gorgias stated that nothing exists, if anything does exist, it is unknowable, if anything can be known, knowledge of it is incommunicable. At a first glance, this may sound like a defeat for scientists. On the contrary, it introduces some basic questions which are often scarcely appreciated by many students, who seem careless regarding the actual nature of their data and about the actual target of their researches. Several famous approaches have been promoted in searching for the actual relationship between Nature and Science. Plato's interpretation of the universe suggested that a world of ideas is the source of a typological nature producing reality. Aristotle's perspective described a universal nature existing regardless of our perception of it. Accordingly, scientists are those explorers who observe and describe this actual reality. Significantly, both these perspectives share the possibility for human beings to attain knowledge of Nature as an actual product liable to be tested.

In contrast, the formalistic approach, developed by Immanuel Kant two thousand years after, proposed a reality organised by a universal human mind. Nature would then be the product of a process of categorisation, and Science would be the recognition of this product. Thus, knowledge depends upon the interpretation of Nature, and scientists are probably those people who find a way to represent and code this perception. This shift represented the main historical rupture with the objectivistic approaches of the classic epistemology, introducing the *subject* as the principal source of knowledge.

Karl Popper, who ten years after his death is still rarely read by many biologists, proposed a useful and pragmatic synthesis (Popper, 1959). Actually, reality may be "true". And this truth can be reached and known by the human mind. What cannot be reached, is the absolute certainty of having attained that truth. This resembles the legendary Babel library, that held every possible book, including your own biography with its future events. You can keep on searching for that book, but you'll never be sure to have found your biography, or its opposite, or one of its innumerable alternative versions. Thus, a fallible knowledge of an objective reality. According to the Popperian paradigms, a theory replaces another when or if it explains a larger percentage of facts, or it is better verifiable. Better yet, if, beyond being verifiable, it is more difficult to falsify. Thus, at the end we must assess that theories are nothing other than hypotheses: they need to be verifiable, and - most of all - they are temporary. Theories only live till they are falsified and substituted.

We can assume that Nature produces facts. These facts then fall into in a process of interpretation, by which different hypotheses are produced and eliminated according to their "cultural fitness". This is Karl Popper's approach to knowledge as a *natural selection of hypotheses*, involving both gradual and punctuationist patterns. The final and current product of such selection is called "Science".

Returning to our original problem, we can consider both of the possibilities: reality is an objective entity, or, conversely, it is a product of the mind. In the first case, considering the impossibility to attain the certainty of my knowledge, *interpretations* of the natural objects and dynamics are "safer" and more cautious tools than absolute descriptions. That is, it is better to generate a *model* that interprets my data and represents the underlying reality, than to have the presumption to have described Nature. The first approach is verifiable; the second is not. In contrast, if Nature is but a projection of the mind, models are the only possible tools to understand its facts. The pragmatism of this formalistic integration can be synthesised this way: although it is impossible to know if my solution is right or true, I can know if it is more or less useful or adequate. Most of this reasoning is based on the assumption that one of the most important features of our sciences and researches is their usefulness. An

achievable interpretation is better than an impracticable truth.

The Web of Life

J.H. Poincaré stressed that it is not possible to know the single entities, it is only possible to know their relationships. This is particularly appreciated by geometric morphometric students working with landmark-based approaches: "form" is but a network of structural and geometrical relationships. The dissection of processes is often necessary in an experimental setting, but it produces artificial systems with different properties from those in the original context. Interestingly, this is also the basic approach to the concept of "relation" in Hegel, who extends this interpretation not only to knowledge but also to reality itself.

Biology often deals with relationships. In particular, evolutionary biologists often deal with phylogeny and with "trees", accounting for some of these relationships. The classical bipolarism in comparative biology describes an antagonism between the phenetic and cladistic approach. The first is assumed to describe the variations in phenotype (thus, the final product of the integration between genes and environment), the second to describe the phylogenetic relationships. Although the differences between the phenetic and cladistic approach are well known and discussed, the similarities are not. Actually, both approaches are used to interpret the natural diversities and relationships, by representing the sharing of a "structure" or of a "process" respectively. Phenetics represents the sharing of a structural network (more than simple "physical" features), cladistics, instead, represents the sharing of a sequence of variations (more than phylogeny itself). If something "represents" something else, it is "a model". Both, thus, are models to represent *affinities*. Phylogeny is something that does exist, independently upon our hypotheses. What is more important, phylogeny is "one", independently upon our current knowledge of it (Bruner, 2004). In contrast, cladograms and phenograms are "many", as much as is possible to achieve using different algorithms, characters, loadings, polarity, character coding, operational taxonomic units, and software.

Cladograms and phenograms are ordinations of reality. They are neither true nor false, but simply display compared variations according to our *a priori* assumptions. Phylogeny is something that can be hypothesised (with falsifiable hypotheses) to integrate the information regarding morphology, genetics, ecology, physiology, biochemistry, and ethology, that we obtain using the human unique cognitive capacities, and not as results of algorithms and computed ordinations. Things become even more difficult when dealing with paleontology (Trinkaus, 1990), especially in considering Primates: the substantial specimens currently acknowledged in the paleoprimatological fossil record might account for 1% of the entire extinct variability (Martin, 1990). Too few to let the software run freely.

From Nature to Science

It may be interesting to try to synthesise what the properties of a model are. First, it is something that *represents* something else; second, it necessarily bears only a fraction of all the *properties* of the system it describes; third, it has been developed for a more/less specific *purpose*; fourth, the fraction of the properties of the original system it describes has been *selected* according to this purpose; fifth, it is characterised by a set of parameters and variables, requiring a set of *a priori* choices and assumptions – thus it has been developed within a specific *environment*; sixth, it can be used only within a specific *range* (physic, geographic, systematic, etc.) in which its properties, resolution, and falsifiability, have been tested.

The reverse is more important: a model should not be used for purposes other than those for which it has been planned, or to consider properties which it does not represents, or outside the environment in which it has been created, or to apply it beyond the ranges in which it has been tested. Finally, a model is neither true nor false, but more or less useful, according to the percentage of data it is able to explain or, better, according to the ratio between the verifiable

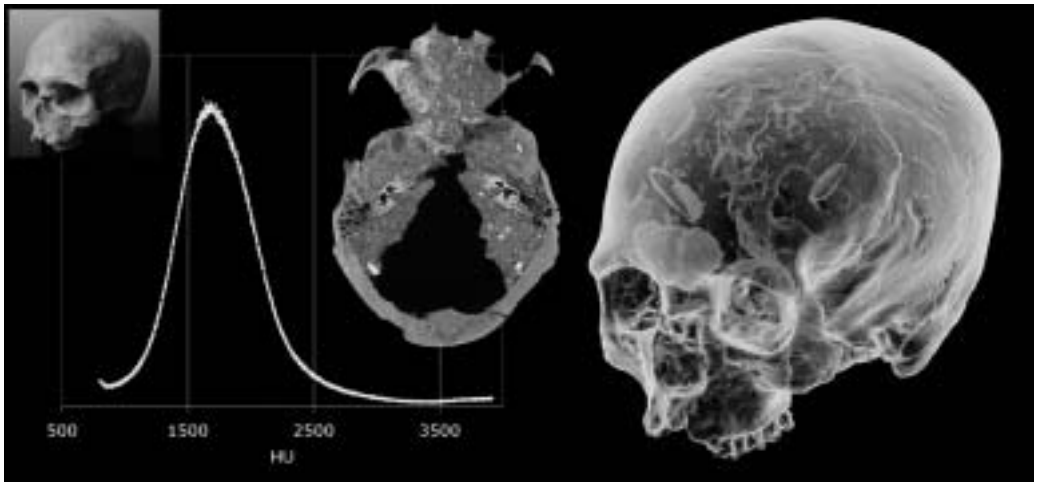


Fig. 1- Computed tomographic techniques produce a digital model of a fossil skull (left top), representing its densitometric properties (synthesised by the attenuation spectrum), and the spatial relationships between its finite volumetric elements, by two- and three-dimensional replicas (from Bruner & Manzi, 2003).

information it involves and its falsified quota. The atom is a model, neither beautiful nor awful, but useful. The DNA helix is a model, neither true nor false, but yet unfalsified. Einstein's energy equation is a model, neither right nor wrong, simply working.

Computed tomography clearly generates digital models (Zollikofer *et al*., 1998; Recheis *et al*., 1999; Bruner 2003b). CT slices and CT surface and volume reconstructions are digital replicas of real objects (Fig. 1). Some properties of these objects (spatial relationships and density of finite volumetric units) are transformed in signals through an X-ray attenuation, captured by a proper receptor, and coded according to international standards (Spoor *et al*., 2000).

In this context, "model" is something easily interpreted. It is more difficult to imagine the same approach for any direct visualisation of reality, from cells to tissues. In reality, computed tomography and histology do not seem to differ substantially (Fig. 2). Both start working from the isolation of anatomical planes, be they physical slices obtained by a microtome or digital sections from a scan machine (the operational problems are obviously extremely similar: composition of the object, slice thickness, etc.). Subsequently, colouring and segmentation techniques are needed to localise specific components of the morphological and anatomical system, be they developed as biochemical markers and reactions or algorithms. Finally, we have to choose the right optics or software, to visualise the final result. Interestingly, both the microscope and the computer screen will surely be the main cause of our eye damages.

With reference to the landmark-based multivariate analyses, the boundaries between reality and its representations can be more confused. The basic procedure in geometric morphometrics (Rohlf and Bookstein, 1990; Bookstein 1991; Marcus *et al*., 1993; Marcus *et al*., 1996; Adams *et al*., 2004) and other geometric-based analyses (e.g. Richtsmeier, 1989; Lynch *et al*., 1996) involve the Euclidean identification of a set of anatomical landmarks (the *configuration*) using spatial coordinates in two or three dimensions. The systems of coordinates sampled from each specimen are superimposed following a certain procedure to minimise and normalise differ-

ences. The residuals are then used to compute multivariate ordination analyses, such as principal component analysis, canonical variates and discrimination analysis, or multiple and multivariate regression. The covariation of landmarks along the resulting morphospace is visualised using interpolant functions, distortion grids, and vectors. Interestingly, after the early conceptual approach proposed by D'Arcy W. Thompson in the first half of the 20th century, primatology was one of the pioneer disciplines to attempt to analyse the morphological variability in terms of landmarks, superimposition, and residuals, long before the development of computed tools (Verheyen, 1957).

Clearly, the *configuration* is a model of the anatomical structure, representing the spatial relationships between some of its components. However, the multivariate shape of space (morphospace) is actually a model in itself: it is generated by the intrinsic structural properties of the original variation, transformed in algebraic covariance through a matrix-based codification. The morphospace represents the morpho-functional system associated with the variability of the sample. Accordingly, the multivariate axes, as algebraic vectors of structural networks, represent models of spatial variation, and the visualisation techniques (deformation grids, chromatic patterns, etc.) represent the Euclidean changes along those algebraic models: representations of representations (Fig. 3).

As any other interpretations of reality our models represent something else (a biological system), they have specific properties (geometrical, spatial), they have been developed for a purpose (comparison), they are characterised by an environment (statistics, algorithms), and they have been tested just within a specific range (the sample). It is worth noting that, although the current geometric morphometrics packages are user-friendly, each passage in the procedure involves assumptions and simplifications, which must be biologically tested and considered. The superimposition itself is sufficient to create a complex interface between science and nature (see Richtsmeier *et al*., 2002).

Konrad Lorenz (1973) proposed *abstraction* as one of the principal integrative functions of cognition, through the process of *pattern matching* described by Popper. Going back to knowledge as recognition of relationships, it is worth noting that he interpreted this function as the expression of *relations* and *configurations*.

Within the context of our scientific purposes, we usually promote a conventional process of

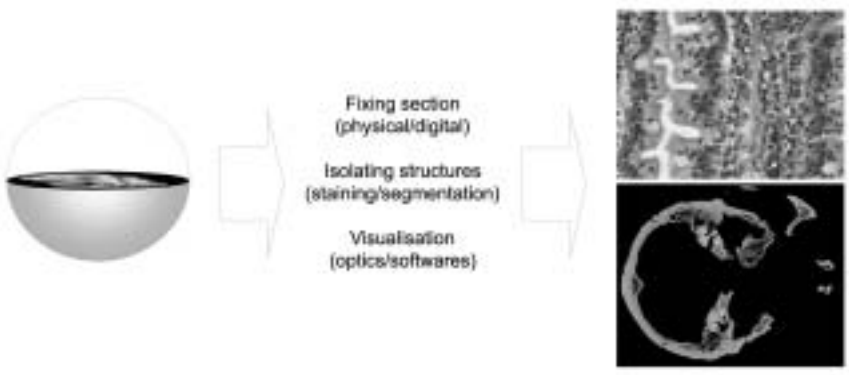


Fig. 2 - histology and computed tomography share the same methodological and procedural approach: producing sections (physical or digital), isolating structures (staining or segmentation), visualising morphology (lens or software).

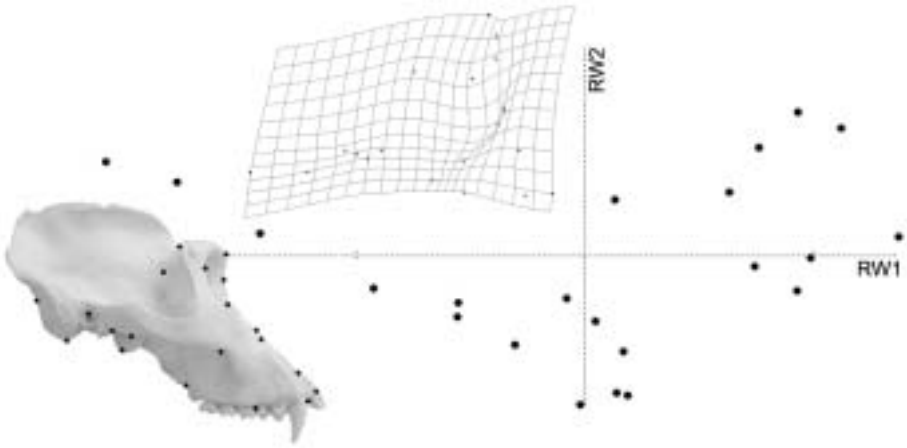


Fig. 3 - Geometric morphometrics techniques produce a statistical/algebraic model of the structural morphological network within a sample variability: the configuration is a geometric model of a morphological system, the morphospace is a model of structural covariation, and distortion grids are models of geometrical changes (from Bruner & Manzi, 2001).

induction. The results which originate from our models are projected onto reality itself. At least, our specific results tend to be generalised to describe the entire problem. This is not necessarily a failure, nor a bias: science works constantly on a retroactive exchange between induction and deduction. What must not be forgotten, is a useful and pragmatic awareness of induction. Grids do warp; skulls do not.

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