



Commentary

On growth and form in the “computer era”: from geometric to biological morphometrics

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Both A.C. and A.L. contributed equally to this paper and to the editing of the “Yellow Book”.

Abstract

Almost 100 years after the publication of Thompson’s seminal book “On growth and form”, the study of animal morphology is becoming again central to biology. This is also thanks to the development of powerful computerized quantitative methods for statistical shape analysis, collectively known as Geometric Morphometrics (GM). GM was announced as a revolution just two decades ago. The “revolution” is now a standard tool in numerical analyses of phenotypic variation in mammals and other organisms. Hundreds of studies are published every year that take advantage of GM (e.g., more than 800 entries in Google Scholar only for 2012). We celebrate the 20th anniversary of the “revolution in morphometrics” (Rohlf and Marcus 1993, p. 129) with the publication of a “Yellow Book”, a special issue of *Hystrix* dedicated to Evolutionary Morphometrics and Virtual Morphology. A series of 14 papers by leading morphometricians summarizes the main achievements in GM (surface methods, comparative methods in shape analysis, phenotypic trajectories quantification, modularity/integration, the use of R in morphometrics), describes its most innovative developments (ecometrics, eigensound analysis, biomechanical GM), and discusses common misunderstandings of well established methods (visualization of shape differences). Besides celebrating the success of statistical shape analysis in biology, this issue aims at introducing to GM readers unfamiliar with or intimidated by its strong numerical background. This is why, as Editors, we asked all contributors to provide concise and accurate but also clear and simple descriptions of techniques and applications. We hope that we succeeded in this aim, and wish that this Yellow Book may help to tighten the connection between biologists and statisticians for a truly “biological” GM.

It is not accidental that *Hystrix*, the Italian Journal of Mammalogy, strongly supported and solicited the publication of this volume on the advances in Geometric Morphometrics (GM – Adams et al. 2004 and Adams et al. this issue) in the last 20 years. Italian theriologists have had a long and strong connection with the “dream team” that led the morphometric revolution in the ‘90s (Rohlf and Marcus, 1993; Corti, 1993). They have also been among the most enthusiastic applicants of the new methods since the early time of the morphometric synthesis (Adams et al., this issue). It is indeed thanks to the fruitful interactions between theoreticians and biologists in Italy and elsewhere that modern morphometrics has become deeply rooted in biology. Even the somewhat old fashioned use of morphology in taxonomic assessment has been revitalized by GM: famously, a study of cranial variation in Old World moles (Rohlf et al., 1996) has become a standard reference in the field (Rohlf, 1998; Viscosi and Cardini, 2011), obtaining almost 200 citations (Google Scholar, January 2013) and becoming a best known early example of the impact that can be achieved when statisticians and morphologists join their forces.

GM is “a collection of approaches for the multivariate statistical analysis of Cartesian coordinate data, usually (but not always) limited to

landmark point locations” (<http://life.bio.sunysb.edu/morph/glossary/gloss1.html>). Greatly inspired by Thompson’s “On growth and form” (1917), GM puts together geometry, multivariate morphometrics, computer science and three dimensional imaging techniques for a powerful and accurate study of organismal forms. Today, it is a leading family of methods in quantitative biology and the type of computerized image analysis which is likely to generate the main source of data and analytical tools in the emerging field of phenomics, the comprehensive study of phenotypic variation and the latest of the “-omics” after genomics, proteomics, metabolomics and all the other -omics (Houle, 2010).

Despite its modern success, however, not that many scientists seemed to have grasped the potential of the new methods in the early days of GM. Especially in Italy, very few biologists were brave enough to venture into its statistical meanders. Marco Corti and one of us (A.L.), theriologists from the University of Rome La Sapienza, strongly believed in the “revolution” and struggled to make it spread across Italy. After a first ground breaking meeting two years before in Ann Arbor (Michigan, USA), they were the only Italian participants to the second GM workshop in 1990 (Stony Brook, USA – Fig. 1). There, Marco and Anna met some of the American “giants” of the methodological development of modern morphometrics: James Rohlf, Fred Bookstein, Dennis Slice and Leslie Marcus. This encounter marked the beginning a long human and professional companionship, as well as of a series

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of memorable methodological discussions, which led to common projects, joint papers, and fundamental advancements.

Indeed, the “partnership” between morphometrics and Italian theriology has a long history (Corti et al., 2000), and one that continues today. The fifth international Theriological Congress (Marcus and Corti, 1989) hosted what was likely to have been the last workshop (Marcus and Corti, 1989) on traditional morphometrics (Marcus, 1990). Less than 10 years after, another theriological congress, the Euro-American Mammal Congress (Santiago de Compostela, Spain, 1998), was home to another morphometric workshop, but, this time, one entirely devoted to the use of GM in mammalogy (Corti et al., 2000). This workshop led to an edited volume, published in *Hystrix* (<http://www.italian-journal-of-mammalogy.it/issue/view/264>), which included seminal papers, such as Rohlf’s (2000) contribution on the theory of shape spaces, and Marcus et al.’s (2000) examination of the applicability of GM to craniometric data spanning the whole range of variation of placental mammals. This pioneering research paved the way to an exponential increase in the use of GM in mammalogy and other fields of biology (Adams et al., 2004). Those early studies contributed to a better understanding of the methods and their applications, and a long series of international workshops helped to make GM not only better known to the scientific community but also more accessible to biologists. Indeed, all these meetings were characterized by a strong focus on practice and several of them were held in Italy (e.g., Ciocco, 1993; Rome, 1997-2002; Turin, 2008; Genova, Firenze and Pesche, 2010 – Fig. 1).

A pivotal role in the first decade of the “morphometric revolution” was played by James Rohlf. Among his many merits, he contributed to propel the field by ‘translating’ (e.g., Rohlf 1993) Bookstein’s theoretical advancements, famously as brilliant as cryptic, into a form intelligible by biologists, who often lack the gift of intuition of numerical abstractions and seldom have an adequate background in mathematics. Rohlf was a “translator” for biologists also in another sense: he developed a variety of user-friendly and free GM programs, which over time became known as the tps Series (tpsDig, tpsUtil, tpsRelw etc. at: <http://life.bio.sunysb.edu/morph/toc-software.html>). Rohlf’s software was likely the most broadly used in the ‘90s and is now one of the programs that enabled the biological community to take its first steps in the complex multivariate shape space first described by Kendall in the ‘80s (Slice 2001, and references therein). It is a fact that this increasing availability of user-friendly GM programs has been and still is a double-edge sword. It might lead users to do things that they do not understand and to treat analytical methods as a black-box. However, it is also undeniable that the success of GM in biology owes much to free software developers, and the range of programs that now goes from comprehensive easy-to-use executables, such as MorphoJ (Klingenberg, 2011), or the IMP series (Sheets and Zelditch, this issue; Zelditch et al., 2012), to powerful and flexible routines in R (Claude, 2008, this issue; Adams, Otárola-Castillo, 2013). Detailed user guides and introductory manuals (Zelditch et al., 2004, 2012; Claude, 2008) for biologists also played an important role in making GM less intimidating to the non-numerically oriented scientists.

The theoretical development of GM is far from over. New methods and innovative applications are constantly appearing in the literature. We are also reaching a much better understanding of the “old” methods, including some potential pitfalls frequently overlooked even by expert practitioners. For instance, visualizing shape variation with thin plate spline deformation grids, outline or surface rendering, and displacement vectors have become almost default options in biological GM. However, each of these methods has some largely under-appreciated limitations, but no clear and simple discussion of their advantages and disadvantages (Klingenberg, 2013a, this issue). It was also to fill some of these gaps in the literature, and to provide state of the art reviews and examples of GM in evolutionary biology that we decided to invite leading morphometricians to contribute to this special issue of *Hystrix* on “Evolutionary morphometrics and virtual morphology”. We did choose, however, not to exclusively focus on GM, as GM belongs to a much broader family of computerized methods for quantitative mor-

phological investigation (e.g., Evans’ ecometric shape descriptors this issue).

Adams et al. open the volume with a broad overview of the field. The paper is the long awaited update of their famous “10 years from the revolution” paper (Adams et al., 2004): also “born” in Italy, as a contribution in the proceedings of the Rome 2002 morphometric workshop, Adams et al. (2004) has now been cited more than 600 times (Google Scholar, January 2013). After readers are introduced to the concept of the “Procrustes Paradigm”, have discovered what is new in the field, and what they can expect to see in the near future, 13 papers, among them reviews and example studies, offer a detailed presentation of some of the main methodological advancements and “hot topics” in GM research in mammalogy and evolutionary biology.

The reviews focus on a disparate set of methodological issues. We hope they will benefit readers with their up to date information. Also, and more importantly, their aim is to provide clear discussions on technical aspects, as well as simple explanations of the pros and cons of different methods, and brief recommendations for the less experienced morphometricians. The first review (Klingenberg, 2013a, this issue) after Adams et al., however, might come as a surprise. It is on a topic which most practitioners do not find particularly hard to get, and actually it seems one of the most intuitive aspects of GM: the visualization of shape differences. Klingenberg carefully shows that this is something in fact far from obvious. Whether we use grids, vectors or other diagrams, and how we should interpret them, might represent the most overlooked and misunderstood issue in modern morphometrics. Also, as the author’s acknowledgements suggest, it is an issue that may have unexpected consequences even for... airplane passengers!

As the title of this volume implies, morphometrics has been traditionally employed in evolutionary studies and this is still, very likely, the main field where GM finds its most enthusiastic users. This makes a vast number of GM analyses “comparative”, and comparative data generally require a special statistical treatment. Monteiro reviews how one might take phylogeny into account in GM studies and why this is important. Polly et al. show that even an apparently straightforward principal component analysis (PCA) may be performed within a phylogenetic framework. A variety of “comparative methods” has been developed over the last three decades to address the non-independence of observations due to phylogenetic relationships. These methods are now routinely applied in ecology and ethology, and have become more popular also among morphometricians especially in the last few years. Their use, however, raises non-trivial questions and may not always be as simple as one might wish. This is partly because of the multivariate nature of shape data and therefore the need of multivariate extensions of univariate methods. Monteiro provides a broad and careful overview of the field within the context of statistical shape analysis, and makes several suggestions and recommendations including tips on the software for performing GM comparative analyses. Polly et al., in contrast, focus on a more specific and fairly recent development: the use of phylogenetic comparative methods in PCAs. They exemplify phylogenetic PCA (pPCA) using both simulated and real data (carnivoran humeri), and suggest where the main differences are compared to a standard PCA. For instance, Polly et al. demonstrate that pPCs are not uncorrelated, but do preserve original shape distances and therefore any potential phylogenetic signal in the data. Also, they may have a profound impact on specific analyses, such as tests of modularity using eigenvalues.

Modularity and integration is now a central topic in evolutionary developmental biology (evo-devo), and one that must be investigated at all levels: from genes to individual organisms and specific and supra-specific taxa. (Klingenberg, 2013b, this issue), who has been a pioneer of this type of studies using GM, summarizes the all the different methods that have been employed until now to test modularity and integration. He reviews what their application to a variety of groups of mammals has taught us, and shows also how examining symmetry vs. asymmetry might help to infer the strength of modularity and integration. Even more importantly, he opens the discussion on one of the

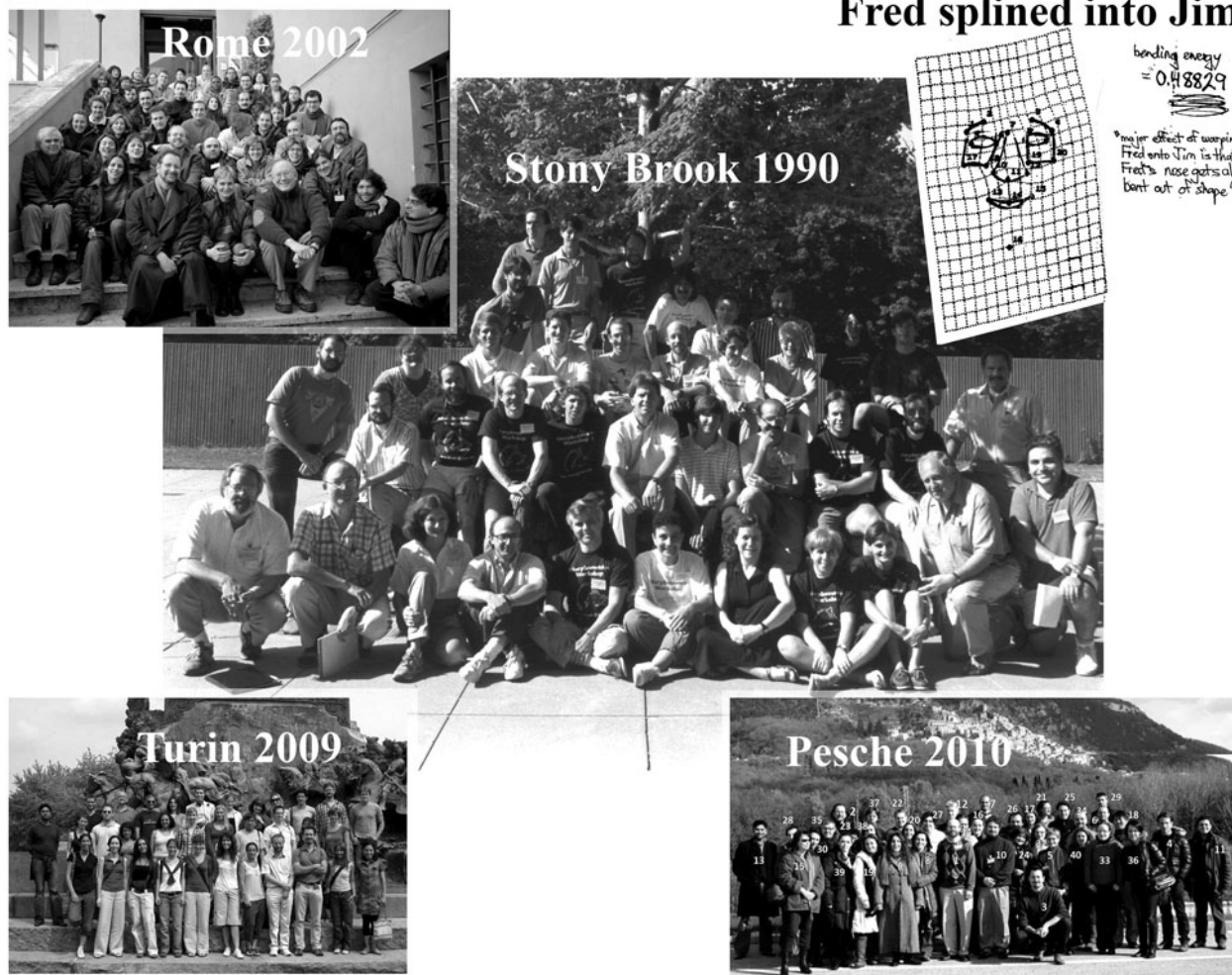


Figure 1 – Group pictures from the “historic” workshop held in Stony Brook (1990) and three of the several GM workshops held in Italy. In the top left inset, the “Bookstein to Rohlf” face-warping diagram sketched as a joke by one of the Stony Brook workshop participants.

most pervasive aspects of shape variation, with a central role as an integrating factor: size-related shape variation or allometry.

In the next contribution, Mitteroecker et al. describe how to study allometry using accurate multivariate methods, and also show how to effectively visualize size-related variation in shape. They suggest that there might be several ways for estimating and comparing allometries, including regressions and form spaces (Dryden and Mardia, 1998). Finally, they exemplify these methods on real data. By exploring how faces vary in humans in relation to factors such as body height, they demonstrate that GM is not limited to the analysis of hard tissues and, intriguingly, find that shorter men tend to be more childlike in facial features.

Measuring allometry and estimating its significance and magnitude is a first step, which is often followed by tests of differences in allometric vectors (e.g., men vs. women, humans vs. chimps etc.). Generally, whenever shape trajectories are compared, different aspects might be considered such as direction, overlap, length, start and end points. Probably the most traditional method to test trajectories across groups is a multivariate analysis of covariance (MANCOVA – e.g., Viscosi and Cardini 2011), a technique available in most statistical packages. However, MANCOVAs only compare the direction of within-group covariation and overlap between groups, and generally do so by performing parametric tests. MANCOVAs, as well as tests of vector angles, length etc., can be performed using resampling statistics. Resampling methods make fewer assumptions than parametric tests, and are generally more suitable to highly dimensional data and relatively small samples. A multiplicity of resampling techniques have been proposed in GM to

test trajectories. However, nobody has yet offered a synthetic and updated overview of these methods. Sheets and Zelditch, in this issue, fill this gap with great completeness. As in their introductory book on GM for biologists (Zelditch et al., 2004, 2012), they guide the reader with clarity through a maze of statistical methods, in which a biologist could easily get lost.

Collyer and Adams carry on discussing how to study phenotypic trajectories but they take a novel and broader view. Framing scientific questions in terms of trajectories allows to test not only group differences in multivariate spaces (“static” approach) but also differences in the ways groups change positions in relation to ecological or evolutionary gradients (“dynamic” approach). With this dynamic measurement of change, “raw data” become similar to series of shapes in locomotion analysis, where locomotory trajectories are represented as forms whose size, shape and main axes of variation can be quantified and compared in a GM framework (Adams and Cerney, 2007).

Collyer and Adams’ methods might be soon become another tool for investigating what set the main direction of morphological evolution in mammals, the main focus of Renaud and Auffray’s contribution. Using teeth and mandibles of murine rodents, they provide inspirational insight into how shape analysis might help us to link micro- to macro-evolution. By testing lines of least resistance, that might channel but potentially facilitate change, Renaud and Auffray produce results that can be help to design future experimental studies and explore the processes behind the main phenotypic patterns they measure in mice.

Murine rodents are a most common study group in GM research, and also the subject of the paper by Claude. His aim, however, is different:

Claude, the author of *Morphometrics with R* (2008), examines the discriminatory power of different morphometric descriptors and analytical methods, when closely related species are compared. By doing this, he shows how to carry on these analyses in R, possibly the most widely used statistical environment in science. Claude convincingly makes the point that, despite a steep initial learning curve, investing time to learn how to perform GM analyses in this free open source software may be worth the effort, and rapidly lead to flexibility and a range of potential applications hardly matched by any other program.

The next three contributions are very heterogeneous. All of them represent innovative extensions of GM methods. Renaud and Auffray, as well as Claude, have provided examples of analyses of outlines using Fourier methods. These methods, which pre-date the “Procrustes Paradigm”, have been fruitfully employed for at least three decades to measure outlines. Outlines, and more generally curves and surfaces, tend to lack landmarks with a straightforward and precise correspondence across individuals. In the '90s, however, Bookstein and colleagues (references in Gunz and Mitteroecker this issue) showed how curves and surfaces can be also measured using Cartesian coordinates of points within a Procrustean framework. They suggested elegant algorithmic manipulations to improve the mathematical correspondence of a special type of points, called semilandmarks, employed to “discretize” variation in forms without landmarks. Although there is no biological model behind these algorithms, and answering the question of the biological correspondence of semilandmarks is far from trivial (Klingenberg, 2008; Oxnard and O’Higgins, 2011), semilandmark methods have allowed morphometricians to combine landmarks and points on outlines or surfaces in a single analysis. Semilandmark methods have thus opened a huge range of analytical possibilities that few morphometricians could review better than Gunz et al. These authors belong to the “Viennese school” of morphometrics, which largely developed semilandmark and surface analyses and massively applied them in anthropology. In their review, they explain methods and applications in two and three dimensions, and discuss how semilandmarks can become part of a larger set of tools used for estimating missing landmarks in incomplete specimens, as in the recently born discipline of virtual reconstruction of fossils (Gunz et al. 2009, and references therein). Semilandmarks represent a fundamental step forward in shape analysis, and one that is rapidly gaining popularity thanks to a user-friendly implementation in 2D by Rohlf (<http://life.bio.sunysb.edu/morph/morphmet/tpsrelww32.exe>). More recently, free scripts and packages for 3D analyses have also been released (see documentation and files at: <https://sourceforge.net/projects/morpho-r-package>, <http://CRAN.R-project.org/package=geomorph>, <http://hdl.handle.net/2022/14613>). As these new possibilities arise, the nicer visualization and apparent increase in information might tempt users to add semilandmarks without a proper consideration of whether they really matter for a specific study aim. More (points in this case) may not always be better, and, as it happened in the past with the interpretation of the biology (or lack of it) behind partial warps (Rohlf, 1998), time will help to better understand how powerful mathematical methods for the GM analysis curves and surfaces relate to underlying biology (Klingenberg, 2008; Oxnard and O’Higgins, 2011; Viscosi and Cardini, 2011).

In the next two studies, MacLeod et al., and O’Higgins and Milne, show that GM is not only extending its analytical toolkit, but also is taking directions which few might have predicted. MacLeod et al. argue that sounds can be measured as 3D shapes. By doing so, in their eigen-sound study, they manage to discriminate bat species with a high cross-validated accuracy ($\geq 80\%$). This is better than using traditional acoustic analyses and suggests a potential for innovative GM applications, well beyond the traditional range of morphological investigation. Indeed, this is also what O’Higgins and Milne demonstrate in a rather different context: the functional and biomechanical study of armadillos’ femurs. The authors use functional simulations and techniques from mechanical engineering to measure the biomechanical performance of the femur. This first type of analysis produces deformations in a computerized 3D model of the bone. The resulting ‘deformed’ virtual bones

become new shapes, and these can be compared and visualized using GM. This new tool might open “new avenues of investigation of skeletal form and function in evolutionary biology” (O’Higgins and Milne, this issue), although, as for semilandmarks and eigen-sound methods, there might be a lot that we need to learn on validity and accuracy, and the correspondence between these numeric representations and their underlying biology (Adams et al. this issue).

Last but not least, Evans stimulates the reader to keep her/his mind open and not to be led by a preferred or fashionable set of methods. He urges to go beyond the boundaries of ‘standard GM’ and explore the usefulness of other shape descriptors to investigate specific questions on function, ecology and the interactions between organisms and their environment. Using examples from extinct mammals, Evans points out that hard tissues and especially teeth (the most frequently preserved component of the mammalian fossil record) have much to say on how species evolved and adapted to the environment. He reviews a variety of shape statistics, which do not encode shape itself, such as shear ratios, measures of wear, relief indexes, fractals and other measurements of sharpness, complexity, height and curvature of cusps. Thus, after Gunz et al. (this issue) have shown us how to numerically build virtual fossils, Evans demonstrates that a combination of biological insight and sophisticated quantitative analyses of forms can help to reconstruct palaeo-environments of extinct forms.

“Virtual morphology and evolutionary morphometrics” celebrates the 20th anniversary since the “revolution in morphometrics” (Rohlf and Marcus, 1993), and the enthusiasm with which Italian theriologists joined this revolution. This special issue of *Hystrix* will be probably known as the “Yellow Book”, following a long tradition of naming GM books after the colour of their covers. It is our wish that the “Yellow Book” will make the enthusiasm for GM even more contagious, and contribute to increase the number of biologists that, like us, believe that times are mature for a more profound integration of biological knowledge and numerical methods in the transition from geometric to biological morphometrics (Oxnard and O’Higgins, 2011).

Some of the readers will be fascinated by these methods, but also intimidated by the complex theory of multivariate statistical shape analysis. As biologists, we have shared and still share these feelings. However, we have also learnt that the morphometric community is a great source of friendly and precious advice. The readiness with which the “Giants” of GM accepted our invitation to contribute to this volume went beyond our expectations. We do hope that the “Yellow Book” will provide beginners and less experienced morphometricians with easy-to-follow introductions to the most modern methods in morphometrics. However, this volume will not and cannot answer all questions. As James Rohlf said in a memorable workshop in Rome ten years ago, beginners should not be shy and, when they cannot find clear explanations in the literature, they should look for help in MORPHMET (the discussion list of morphometricians: <http://morphometrics.org/morphmet.html>), by directly contacting colleagues or by attending one of the many GM courses and workshops, which are now run regularly in many countries (<http://life.bio.sunysb.edu/morph/notices.html>).

Finally, this volume gives us a chance to remember a few friends, who are no longer with us: Marco Corti, Robin Hennessy, Les Marcus and Santiago Reig. They were all passionate scientists, keen pioneers of “biological GM”, loving friends and great mentors. Santiago’s memories of Marco and the early days of GM, a few years before Santiago’s death, are testimony to both the great enthusiasm and the friendship we and many others experienced in the morphometric community. ☹

MORPHMET

Re: Marco Corti: 1950-2007
Tue, 13 Feb 2007

“It was a big shock and extremely sad news to hear that Marco is not with us anymore. For those that witnessed the enthusiastic beginning of the “GM revolution”, Marco was always the reference-guy for many of us that were on the most zoological side of the crowd. Although definitely a tool-user, Marco was among the advanced and smart users, much more confident on math and stats than the rest of us, and also truly proficient on SAS, a great deal of this learned directly from Les

Marcus. That is why he often played a role as the connecting liaison between developers and clients at the various morphometrics symposia and workshops during the 90'. If you didn't get something during the lecture, you still had the chance of learning it after-hours from Marco, in plain words and using friendly examples... If he admitted that he didn't understand something very well, then forget about it, there'll be little chances that you'll get it... but hey, knowing that Marco was also lost in that something, would make you feel less frustrated about it. Marco managed to be the first one (together with Anna Loy, most of the times) to put into practice and publish papers using the latest morphometric techniques applied to the kind of evolutionary problems of mammals that we all had in mind. In that way he was a pioneer, clearing the path and serving as an inspiration for many mammalogists. His papers were a model to follow because he showed us how to put into practice methods that seemed so complicated and unreachable for many of us that we would have never dared to use, had it not been for his papers. And above all, Marco will always be remembered as the happy man, the happy man who was always smiling and willing to share his discoveries, to show everyone else around him, the exciting and friendly side of morphometrics. We'll miss a generous friend and a most stimulating colleague.”

Santiago Reig (1958-2011), Gregorio Marañón Hospital, Universidad Complutense de Madrid, Medical Imaging Lab

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