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INTRODUCTION TO THE SYMPOSIUM: GEOMETRIC MORPHOMETRZCS IN MAMMALOGY

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Almost twenty years ago Neff and Marcus (1980) distributed a manual containing a synthesis of multivariate statistics and traditional morphometrics at the Rhode Island meeting of the American Society of Mammalogy. It summarized the main multivariate techniques used to investigate variation of linear measurements in mammals, and also included a short description of some of the early ideas of Fred Bookstein on the geometry of size and shape using landmark morphometrics. Since then, there have been a number of workshops and symposia on morphometrics of special interest to mammalogists.

The workshop held during the fifth International Theriological Congress (Marcus and Corti, 1989) was the last one to emphazise traditional morphometric methods. It also included an introduction to cladistic software. Starting in 1988 a number of symposia and workshops were held on the new or geometric morphometrics, some of which were published as a series of colored books – "the blue book" (Rohlf and Bookstein, 1990) from the Michigan Morphometrics Workshop in 1988; "the black book" (Marcus et al, 1993) from the workshop in Valsain, Spain, and the "white book" (Marcus et al, 1996) from the NATO Symposium on Advanced Morphometrics in Il Ciocco, Italy, 1993. The colored series also includes "the orange book", the monograph by Bookstein (1991) that together established the basis of a landmark morphometric toolbox that replaces much of what Marcus (1990) called "Traditional Morphometrics". More recently, at the Morphometrics Symposium of the International Congress of Systematic and Evolutionary Biology, held in Budapest in 1996, five of the nine papers pertained to mammals (Klingenberg and Bookstein, 1998). The first paper in that symposium pointed out that the morphological synthesis has been established (Bookstein, 1998), and it was time to shift to applications of (geometric) morphometrics in various biological disciplines. At that meeting and here at this symposium there are papers discussing the acquisition of data, sources of error, and systematic problems in mammalogy.

In spite of proposals such as Schluter et al. (1997) for using maximum likelihood methods to estimate ancestral values as a way to integrate morphometrics and phylogenetic analysis, the approaches advocated and applied in other earlier papers (for example Voss, 1988) was to map morphometric variation onto a known phylogeny

(Klingenberg and Bookstein, 1998), and not to construct phylogenies from morphometric data. In fact, Marcus and Corti (1996) pointed out the frustration on the part of systematists over how landmark morphometrics could be applied to cladistics, and the lack of interest or opposition to these applications among the developers of the methodology (Bookstein, 1994). In 1999, the Systematics Association held a symposium in Glasgow on the topic "Morphology, Shape and Phylogenetics" in August (http://www.nhm.ac.uk/palaeontology/meetings/samp/samp.htmlweb site), and a running debate continues.

This special issue of Hystrix, Italian Journal of Mammalogy, presents the proceedings of the Geometric Mnrphometrics Symposium held at the 1998 Euro-American Mammal Congress at Santiago de Compostela. All presentations mainly focused on problems in mammalogy and how morphometrics can clarify analyses. The paper by Swiderski et al. uses geometric morphometrics to do a phylogenetic analysis following earlier work (see references in Swiderskij. In addition, two of the papers are of broader interest for geometric morphometrics: one explores shape space models, and the other tests some **of** the assumptions of widely used methods. Accompanying the symposium were posters, and demonstrations of morphometric hardware and software. Image capturing devices, including the Pixera video camera, and Fadda and Corti's device for 3D (Fadda et al., 1997), together with electronic calipers and interfaces for PC's were demonstrated. Morphometric software was available for evaluation, including Rohlf's TPS series and Slice's GRF-ND and Morpheus (all free and available at http://life.bio.sunysb.edu/morph).

The symposium began with the contribution by Rohlf, which discusses shape space models. These models are a key part of the synthesis (Bookstein, 1998), and underlie all applications in landmark morphometrics. Concentrating on triangles of landmarks, the only figures whose shape space model can be visualized, Rohlf discusses the relationships between curved shape space, Kendall shape space and tangent space. He coinpares the curved shape space of generalized least squares (GLS) or generalized Procrustes analysis (GPA), and its projection into tangent space. Another commonly used method for comparing landmark configurations is empirical distance matrix analysis **(EDMA).** Rohlf also illustrates shape space models for triangles implied by EDMA-I and EDMA-II test statistics (see references in Rohlf's paper). More recently Rao and Suryawanshi (1996) have analysed interlandmark distances using log size-scaled distances. Rohlf also illustrates the shape space implied by this approach, and another suggested by Rao and Suryawanshi (1998) that uses differences in angles between lines connecting pairs of landmarks (see Rohlf's bibliography). Rohlf shows that methods which do not depend on Procrustes distances can result in strange shape space models. Furthermore, multivariate statistical analysis based on these alternative methods may give misleading results. The software TpsTRI used to produce the figures shown in the paper is available at **http://life.bio.sunysb.edu/morph,** and provides morphometricians with a tool to experiment with all of these models, and better understand shape and tangent spaces and their geometry.

One question that has been of considerable interest to theoreticians as well as practitioners of morphometrics is "how much variability can there bc in shape as summarized by landmarks when we project into tangent space", the Euclidean space in which we apply classical multivariate methodology. This has not been well determined for practical purposes, though Rohlf has shown that for data sets presented to him, the correlation between Kendall Shape Space Distance and Tangent Space Distance was always very close to one. Marcus, Hingst-Zaher, and Zaher present a comparison of distances from a curved shape space model based on GLS to those obtained using approximations in tangent space for representatives of the orders of mammals. This analysis uses another Rohlf program TpsSmall (also available from Stony Brook). They recorded 35 three dimensional landmarks on skulls with attached jaws. There is greater taxonomic and shape variation in this data set, than present in known earlier studies. One might expect that so much variation would lead to unacceptable distortions in shape comparisons in tangent space. Perhaps surprisingly, but not too much so, they found that the tangent space distances between species over orders provided satisfactory approximations for Procrustes distances in the curved space of GLS aligned specimens. As the sampling involved most of the orders, the authors were also interested in whether there was phylogenetic information in landmark configurations, and say that shape characters based on landmarks are like any others. They also discuss the theory underlying the use of landmark data for cladistic analysis.

Swiderski, Zelditch, and Fink are among the pioneers in application of landmark morphometrics to cladistic analysis (see Swiderski et al. bibliography). In this symposium they provide an application of landmark morphometrics to phylogenetic relationships of some Marmotine squirrels, based on skulls. They illustrate their methodology with a simpler example using triangles and Bookstein shape coordinates. The Marmotine example and earlier published phylogenies use partial warps, and partial warp scores to find and code characters for cladistic analysis. The paper is a clear exposition of their methodology. Two points in their methodology have been criticized in a paper by Rohlf (1998): one relates to the choice of the reference specimen in the analysis and the other to the use of Partial Warps to find characters for cladistic analysis. Rohlf has discussed the distortions in tangent space introduced when the reference is not the consensus or average specimen. Partial warp scores are dependent on the reference whose principal warps provide the basis for tangent shape space. In addition, Rohlf (1996) has questioned whether there are biological signals in the partial warps, as they represent a somewhat artificial and arbitrary decomposition based largely on the reference's principal warps. In their rebuttal to Rohlf (Zelditch et al.,1998) and here in the symposium, Swiderski et al. point out that a reference based on the consensus or average specimen in the study does not represent a real object, and that as long as their characters are comparable and provide clear descriptors of shape differences, they can be coded and analysed cladistically. The characters can then be evaluated in terms of their consistency with other such characters.

All of the remaining contributions represent applications of geometric morphometrics to sexual dimorphism, development, and systematic questions in Mammalogy. Hood's paper on sexual size dimorphism shows that geometric morphometrics is an useful tool to depict shape changes associated with size, with intraspecific and interspecific examples. Using both linear (traditional) measurements and centroid size (the "geometric size variable" provided by geometric morphometrics) he dissects sexual size dimorphism and geographic variation in muskrats, as well as shape differences associated with size evidenced by thin-plate splines. At the interspecific level, comparison of size and shape among several different bat species showed similar patterns of sexual size dimorphism for centroid size and body mass, following Rensch's rule. He demonstrates that geometric morphometrics provides a richer approach to studies of sexual dimorphism than does traditional morphometrics.

Another area of considerable interest is the use of landmark morphometrics in studying development. Zeldtich et al. (1993) again provided early and important applications in Mammalogy, building on the work by Bookstein (1991) on rat calvaria. In this symposium Monteiro describes and compares scapula shape and growth in two species of Dasypodid armadillos and Hingst-Zaher, Marcus, and Cerqueira examine post-natal cranial development in the Sigmodontine *Calomys* ***expulsus.*** Monteiro shows that the amount of shape variation in the two armadillo taxa is partitioned differently among uniform and non-uniform shape contributions. Hingst-Zaher et al. report size and shape changes from neonates to old age for laboratory reared samples from wild caught parents. Using 2D landmarks on dorsal, lateral, and ventral views of the skulls, they were able to show that the majority of shape and size changes occur before 20 days of age, and most of the differences between sexes were due to size. Both studies use thin plate splines to show the differences.

There have been few morphometric studies relating shape to function in mammals. Astua de Moraes, Hingst-Zaher, Marcus and Cerqueira provide analyses of skull and jaw shapes of six Didelphid species belonging to six genera. They recorded 2D landmarks on sizeable samples from both sexes, and were able to interpret shape differences in terms of phylogenetic origin and adaptive zones that the species and their genera occupy. They found that geometric morphometrics provides a powerful comparative tool for such analysis, especially using the graphic visualizations to support their description of shape differences, and multivariate statistics to show the similarity and differences among shapes. They interpret these shapes differences in terms of habits and habitus of the taxa.

It has been difficult to collect three dimensional landmarks on small objects without using expensive equipment. Fadda and Corti built a portable device for recording **3D** landmarks on small rodent skulls (Fadda et al., 1997). The paper by Fadda and Corti, and the paper by Corti, di Giuliomaria, and Verheyen used their device to collect 3D landmarks as part of a continuing application of geometric morphometrics to systematics of African rodents. The paper by Fadda and Corti compare samples from a species complex. They look at shape differences and compare ontogenetic trajectories of centroid size over tooth wear classes. Size differences observed can be interpreted in terms of different altitudes occupied by the species, and shape features are related to predator avoidance for one species. They also contrast the similarities in shape to those obtained from karyology and molecular comparisons. Corti et al. in their study of *Lophuromys* show how size and shape differences relate to growth, sex, and phylogeny in their analysis of the 3D landmarks.

We believe that the use of geometric morphometrics in Mammalogy is sufficiently widespread, that we will routinely see such applications at the mammal society meetings and in the journals of Mammalogy. **As** Klingenberg and Bookstein (1998) point out the applications will penetrate all aspects of quantitative Mammalogy.

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