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GEOMETRIC MORPHOMETRICS –
A contribution to the study of shape variability in Ostracods

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We have told each other so often and with such force and such eloquence of the uses to which the study of ostracodes has been applied that we have overlooked one startling fact: almost no one uses ostracodes for anything.
R.L. Kaesler (1983)

Why shape?

Biodiversity is an issue of main concern not only for scientists but for the whole society as well. Taxonomic richness is but one of the many ways we use to express biological diversity. Morphological disparity – the amount of shape variability within a clade – is another. And given that both features do not necessarily correlate (Cherry et al. 1979, Foote 1993a), their comparison can provide further evidence about ecological and evolutionary processes involved in the production and maintenance of biodiversity.

Morphological disparity can be explored at a wide range of taxonomic levels. Indeed, there has been a growing interest in methods addressing morphological disparity in recent years (Foote 1997, McGhee 1999, Ciampaglio et al. 2001, Wills 2001, Zelditch et al. 2004). Some 'classic' studies concern the morphospace occupied by spiral (Raup 1967) or planar branch systems (McKinney 1981) aiming to understand macroevolutionary patterns at high-rank taxonomic levels. Studies in ecomorphology, however, commonly focus at lower taxonomic levels (mainly, closely related species) seeking for correlations between morphology and ecological requirements (Norberg 1994) or for the effects of competitive selective pressures assumed to occur between (Dayan et al. 1990). At the species level, between-populations disparity and its correlation with environmental conditions is used to evaluate adaptation to local conditions (Loik and Noble 1993); and at further detail, morphological variability within a population can be related to the niche concept and dynamics (Pulliam 1986) or to sexual selection (Møller 1994).

Finally, there is an increasing interest in exploring the potential for shape change of a given genotype – the phenotypic plasticity of morphological features –, as well as its adaptive value (Schlichting and Pigliucci 1998).

The amount of morphospace occupied by a set of clades has been used as indicator of ecological diversity (Warheit et al. 1999), evolutionary radiation (McGhee 1999), morphological convergence in distant communities (Ricklefs and Miles 1994), or selective extinctions (Roy and Foote 1997). Less frequent is its use as tracer of environmental conditions or dispersal routes of groups below the species level (populations, clones, ...).

Why Ostracods?

Most of the issues outlined above can be extensively addressed using ostracods. Indeed, this group of organisms can be labelled as ideal for a morphometric approach because of its high taxonomic richness and the diversity of habitats occupied. In addition, ostracods have an extensive fossil record, a feature that allows the examination of shape-environment relationships back into evolutionary time scale.

Morphometric study of ostracods mainly focuses on the analysis of carapace shape. Ostracod carapace has a marked functional meaning; it is the interface between the organism and its environment (Benson 1981). Hence, ostracod carapaces can be considered as engineering solutions, a compromise between design and materials, developed to match specific environmental conditions (Benson 1981). Consequently, it is assumed that ostracod carapace is subject to selection pressures (i.e. has adaptive value).

At the specific level ostracod carapaces include such a number of features (tubercles, ribs, nodes, spines, …) and are conservative enough to be used for taxonomical identification in both neontological and, specially, paleontological studies. Carapaces, however, are not invariant morphological features at the specific level; indeed, valve shape variability has been extensively documented both within- and between-populations.

Methods for the study of shape change and variability

Form and shape

'Form' is an attribute of organisms that is made of two components: size and shape (Benson 1975, Bookstein 1989, Foote 1995, Baltanás et al. 2000). To discern between 'form' and 'shape' is not a trivial matter given that we frequently deal with information regarding 'shape' which, in fact, is related to 'size' (allometry). This is particularly the case when studying ontogenetic processes or in comparisons between individuals grown under different environmental conditions (Rohlf and Bookstein 1987).

Concerning methods and techniques available for the study of shape change and variability, several approaches exist but we will here concentrate in two: Traditional Morphometrics and Geometric Morphometrics.

Traditional Morphometrics

This approach, also named Multivariate Morphometry (Reyment 1985, Foote 1995) and Multivariate Biometry (Bookstein 1993), is an application of multivariate statistics to morphometric issues. Although widely used, these techniques have a main flaw: they do not recognize de geometric origin of the data under scrutiny. Variables used in this approach — distances, angles and ratios—are out of context both geometrically and biologically (Bookstein 1993). In other words, the set of variables used in these procedures preclude the reconstruction of the original shape out of their values. Such loss of information makes these methods of limited value.

Statistical techniques aimed to study relationships between morphological features (length, height, weight, …) developed well before the term 'biometry' was coined (Galton 1869, 1889). Examples can be found in the works of Montbeillard, Quetelet and Galton; as well as in later contributions by Edgeworth, Pearson, Fisher and Wright.

The many multivariate techniques existing, which have been applied to numerous sets of meristic data derived from a plethora of organisms, emphasize the structure of the covariance matrix over other aspects of the measurements and lack any connection to the geometrical arrangement of such measurements, their biological meaning or the functional processes related to the organism development (Bookstein 1993). Such situation can be noticed in the first publications that use the term 'morphometry' in its current use (Blackith 1965, Blackith et al. 1971).

In addition, traditional morphometrics has some severe limitations (Lestrel 1997): (a) it is highly subjective; (b) it does not preserve information on, *i.e.* it is not possible to recover the original shape out of morphometric variables used (distances, angles and ratios); and (c) all variables used are but a small amount of all information about shape contained in a biological object.

Aware of such circumstances, several scientists (Jolicoeur 1963, Burnaby 1966, Mosimann 1970) tried to put additional emphasis on the biological foundations of morphometric data. Their attempt, however, was not successful enough. The actual turnover occurs at the beginning of the ‘80s with the rise of the so-called Geometric Morphometrics (Rohlf 1990a, Rohlf and Marcus 1993, Bookstein 1991, 1993).

Geometric Morphometrics

Geometric morphometrics inspire, partially at least, in the work of D’Arcy W. Thompson (1942) who approached the study of biological shape change as distortions occurring in a cartesian coordinate system which have been previously selected on the basis of its biological homology. Shape is a definite entity, a configuration of points that keep geometric relationships among them and cannot be split into isolated items (like length or height). Confronted with a biological shape, the morphometrician will attempt to describe it in terms of transformation from an original reference shape. Although the approach proposed by Thompson was very appealing and promising it was not accompanied by any analytical procedure. It was the arrival of the computer age, several decades later, that makes it possible to develop application for morphometric analysis based on Thompson’s ideas feasible (Bookstein 1993).

Within geometric morphometrics, comparisons between organic forms are addressed by collecting information concerning the location of discrete points, called *landmarks*. A set of homologous points, *landmarks*, provides information of the biological form given they are distributed homogeneously on the organism and bear some biological meaning (Goodall 1983, Bookstein 1984, 1986, Chapman 1990, Rohlf and Slice 1990, Schweitzer and Lohmann 1990, Reilly 1990, Bookstein 1991, 1993, Reyment and Abe 1995, Foote 1995, Stone 1998). The analysis of configurations of *landmarks* allows the study of shape change without decomposing it into artificial variables. There are several landmark-based methods (fig. 1) and an updated review can be found in Zelditch et al. 2004. Concerning ostracods, there are several studies that apply landmark methods (Kaesler and Foster 1987, Reyment et al. 1988, Abe et al. 1988, Reyment and Bookstein 1993, Reyment 1995, 1997, Elewa 2004).

For a large number of ostracod species, however, it is not possible to identify *landmarks*, or, at least, a number of landmarks large enough to make that approach feasible. Under such circumstances there is an option: *Outline Analysis* (Rohlf 1990b). Outline analysis operates on the following basis: (1) when landmarks are not available one should record the positions of a rather high number of points along the contour of the studied object; (2) a mathematical function must the be fitted to such observationsin order to (3) explore differences between shapes through the analysis of the mathematical descriptors fitted to them. This approach includes a variety of specific methods (fig. 1), among others '*Eigenshape*' analysis (Lohmann 1983, Schweitzer et al. 1986, Lohmann and Schweitzer 1990), standard Fourier descriptors (Kaesler and Waters 1972), and Elliptic Fourier Analysis (Kuhl and Giardina 1982, Kaesler and Maddocks 1984, Rohlf and Archie 1984, Foote 1989, Rohlf 1995, Lestrel 1997, McLellan and Endler 1998, Baltanás and Geiger 1998).

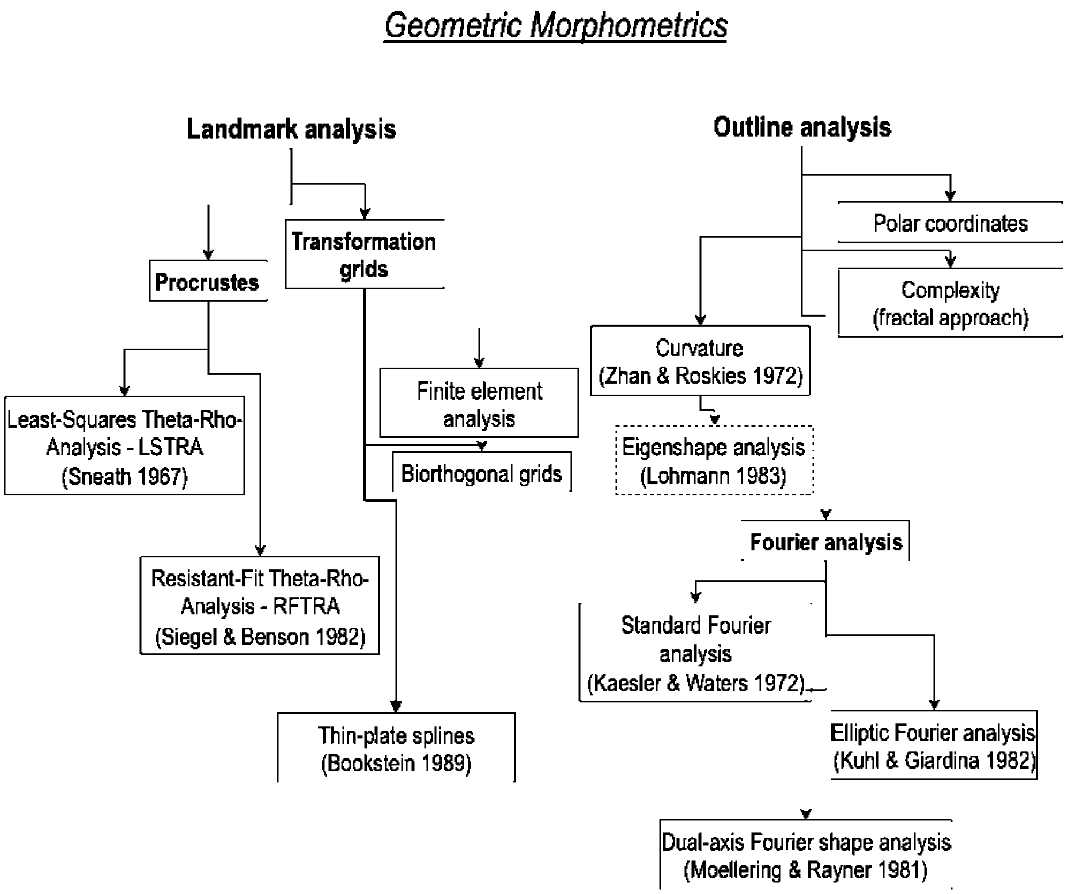

Figure 1: Sketch of relationships between some methods in the realm of Geometric Morphometrics.

Course Outline

Sessions in the course will offer a close view to some of the methods mentioned above together with exercises dealing with related aspects like 'Data Acquisition Procedures' and 'Multivariate Analysis of Shape Descriptors'.

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[*References here included are those mentioned in the text above and many others which have not been explicitly quoted but that might be of interest for those attending the course]

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