Geometric morphometrics simplified
Geometric Morphometrics for Biologists: A Primer by Miriam Leah Zelditch, Donald L. Swiderski, H. David Sheets and William L. Fink, Elsevier Academic Press, 2004. £44.95 hbk (443 pages)
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Although the theory and methods of the relatively new field of geometric morphometrics are becoming well developed (for an overview, see [1]), it has not yet been applied as widely as it could be, owing to the lack of easily accessible introductory guides. This primer, by Miriam Zelditch and colleagues, should make the field more accessible because the new methods described here are relatively simple to apply using currently available software. Geometric Morphometrics for Biologists contains chapters that cover most of the basic topics that a potential user needs to know to collect data in an appropriate format and to use standard multivariate methods for the analysis and interpretation of shape variation.

The authors provide simple step-by-step (‘click by click’) tutorials on the use of morphometric software, starting with the use of the tpsDig software [2] to collect 2D landmark coordinate data and then discussing the use of the many programs in the IMP series [3] to carry out various analyses. In addition to specialized morphometric methods, the authors also discuss significance testing, resampling methods and other basic statistical methods (however, there are problems with their descriptions of confidence intervals and their relationships to tests of significance). The book also includes chapters about disparity and variation, ontogeny and phylogeny, and morphometrics and systematics. These include some detailed examples and suggestions of new methods (not all of which I agree with). There are exercises with answers at the end of most chapters and a glossary of concepts and terms. A limitation of the book is that methods for 3D data and the use of semi-landmarks along curves and surfaces are relegated to the last chapter. Although the acquisition of 3D coordinate data is more difficult that for 2D data and can require more-expensive equipment, it is now becoming standard in fields such as physical anthropology and primatology and is likely to become more common in the future.

Unfortunately, the book is uneven in its presentation. Some concepts are described in such a way that little mathematical background is required, whereas others assume more sophisticated knowledge. For example, Bookstein shape coordinates are described in great detail (over 20 pages) in terms of simple geometric operations. However, Bookstein’s estimate of the uniform component [4] is derived in detail using complex variables (an approach that does not generalize for use with 3D data).

There are also problems in the presentation of some of the theoretical material that might confuse a careful reader. Although much of their description of Kendall’s shape space is clear, there are problems with some of the authors’ descriptions of the relationships between the hemisphere of preshapes aligned to a reference and Kendall’s shape space. For example, they indicate that the equator of the hemisphere for triangles aligned using an equilateral triangle as a reference corresponds to co-linear triangles (in reality, it corresponds to the single shape that is most different from the reference – a reflected equilateral triangle) and that the ‘bottom half’ of Kendall’s shape space for triangles corresponds to just reflections and can, therefore, be ignored (unfortunate advice because real shape differences might correspond to shapes that look like reflections [5]). The authors also indicate that one will get precisely the same results when testing for differences in mean shape whether using multivariate tests based on partial warp scores or by using Goodall’s F-test. This is unlikely in practice because the partial warp scores procedure is based on a linear approximation to Kendall’s shape space, whereas Goodall’s F-test is based on Procrustes distances in the curvilinear space and, more importantly, on the unreasonable assumption that the variation across landmarks is homogeneous and uncorrelated and, thus, can lead to very different results.

There are other more minor problems. The book does not follow the usual conventions of using italics for scalars, lowercase bold for vectors and uppercase bold for matrices, and the symbol \(X\) is used for the expected value (mean) of \(X\). The use of such symbols makes the book more difficult to read. There are also several disconcerting typos (e.g. incorrect degrees of freedom for \(t\)-tests, and omissions in some equations).

In spite of these problems, Geometric Morphometrics for Biologists (which is likely to become known in the field as the ‘green book’) is an important contribution. I am looking forward to an increase in interest in the field as a result of its publication.
Fossils, genes and adaptation

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It is difficult to shun fascination with origins: think of the Book of Genesis, Hesiod’s Theogony, and corresponding narratives that are dear to people of different age, skin colour and religion. In this respect, scientists do not differ much from remaining humankind and still go on searching for the origin of the universe or the origin of life. Or, perhaps, in Charles Darwin’s comfortable company, for the origin of species and the origin of humans. However, what soon appears less comfortable is that Darwin’s quest for the origin of species was, in fact, a quest for the mechanisms of change in animal and plant populations, whereas the centrality, if not even the very concept, of species rapidly faded out from his pages.

Addressing the readers of his magnum opus about the origin of phyla, James Valentine warns that he is using ‘origin’ in the spirit in which Darwin used it: ‘he was not concerned with the ancestry of any given species but in the process that were responsible for how species could evolve.’ The question then is, whether Valentine believes in the reality of phyla. And the answer is, yes and no. Modern systematists trained in the cladistic frame of mind, even if not committed to the rank-free nomenclature of the PhyloCode, would raise their eyebrows, ready perhaps to add that the origin of phyla is to be found in a precise point in time, much later than the Cambrian explosion: namely, in Cuvier’s paper of 1812 [1], where four major groups were first distinguished to include animals whose organization was comparable within each group but not between any two of them. Valentine’s dissenting opinion notwithstanding, the phyla of modern classifications are basically the recent version of Cuvier’s embranchements; that is, clusters of taxa whose anatomy does not offer many opportunities to identify homologies in respect to those in other clusters.

This typological approach was unavoidable when comparative morphology was the single best source of information for the systematist, but things are different today, and Valentine – the title of the book notwithstanding – has indeed produced a wonderfully informative and well written book by mixing together three basic ingredients that are now available: palaeontology, molecular phylogeny and developmental genetics.

During the past decade, other authors [2,3] have produced book-size accounts of metazoan organization, in which the origin and evolution of body plans were considered from the combined perspective of these traditionally distinct research threads, but Valentine’s account is very different from all of them, not just because of the more detailed account of palaeontological evidence, but also because of the more comprehensive and critical presentation of the morphology and embryology of extant metazoans.

Some readers might share my little worry with the dominating adaptationism, according to which the appearance of limbs within Ecdysozoa (the moulting animals, some of which are limbless, e.g. the nematodes; whereas others have limb, e.g. insects and spiders) is explained in terms of increasing locomotory efficiency in increasingly larger creeping organisms, whereas coelomic reduction in adult ascidians is explained as being adaptive to their sessile existence as mucociliary feeding baskets. The problem, here as in most of the literature about ‘origins’, lies not so much in the obviously reasonable search for adaptive scenarios – whose plausibility, however, is all too rarely testable against an independently derived phylogeny – as in the scarce attention paid to the possible developmental origin [4] of the novelties. A coelom is adaptively useful. Good. But where does it come from? How can we explain its first appearance in ontogenetic terms?

The story of animal origin and evolution from a developmental perspective is still unwritten, but the variegated expression patterns of the so-called

References