

This manuscript should have been far more radical than it actually is. I agree with the authors' specific conclusion --- the "findings" of a macrotaxonomical morphometric analysis of bivalves indeed are irretrievably dependent on the researchers' choice of a quantitative approach, and there is no commonality among the range of those approaches --- but I believe the implications of that apercu are far more fundamental than the present manuscript dares to take them. Simply put, the authors should have concluded that geometric morphometrics (GMM) just has no role to play in the macrotaxonomy of the bivalves (or any other high-level clade), as the most crucial of the axioms obviously fails to obtain: there is no underlying geometric manifold to which to refer the "aligned" data.

There are several available alternatives. In my opinion, the most attractive at present for outlines is the method of Anuj Srivastava and colleagues at the University of Florida (Functional and Shape Data Analysis, Springer, 2016), which easily handles the issue of the "beak" (the single landmark here) but completely supersedes any notion of semilandmarks. There is also Norm MacLeod's system "DAISY" for oriented photographs. Other methods of landmark-free outline and surface analysis likewise are well worth considering. The literature of these in the broad domain of computer vision is huge owing to the immense commercial implications, and this paper might have benefitted from an additional co-author who specialized in that topic.

A hint of the missing logic that the paper has chosen not to embrace can be gleaned from a comment in the Abstract here: "Each alignment implies a hypothesis about the ecological, developmental, or evolutionary basis of morphological difference." The sentence is actually backward. One should start with a morphogenetic hypothesis, weave it into a biometric model for covariances among the important biomechanical indicators of such a model (these will in general be different from model to model, from hypothesis to hypothesis), and then operationalize those indicators rather the way that David Raup did half a century ago for the coiling geometry of shells (a missing reference here, by the way). In this domain of application, to a taxonomic range this broad, the word "alignment" cannot possibly mean what the GMM school takes it to mean (a quotient space of equivalence classes of configurations). It must instead be an observation about the organism, either its development or its function, to be embedded in a spatially extended model that, in my view, cannot benefit from any of the tools of today's GMM at all. No, the hypotheses need to be built into the data collection right from the beginning --- reserving them for the analysis phase is just too late.

In short, the authors are pursuing an impossible task: to adapt GMM to their taxonomic domain. It won't work there; it was never intended to work there (I ought to know, since I founded the field); there are many published articles and book chapters already explaining that in fact it CANNOT work there (see e.g. the notes in Section 5.1 of my 2018 textbook, and then consider the example later in that chapter showing how clearly GMM fails to handle even the radiation of the mammalian skull). I admire the authors' thorough review of the quantitative literature of their field. I would counsel a revision stating, as explicitly as necessary, that GMM has absolutely nothing useful to add to this discussion. The person who has said this most clearly, perhaps, is Richard Reymont. He died in 2016, but a manuscript that channeled his innate

skepticism about macrotaxonomy would be welcome. This could be that manuscript, as long as the authors flatly reversed their basic logic to declare the irrelevance of GMM to macrotaxonomy, in view of the obvious inappropriateness of its axioms in that domain.

This is a signed review from Fred Bookstein, the author of the principal missing reference, "A Course of Morphometrics for Biologists," Cambridge University Press, 2018.