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The effect of dominant geometric themes on morphometric analyses (with special reference to coiled cephalopods)

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ABSTRACT

Many of the samples chosen for morphometric analysis represent minor variations on a strongly expressed, single geometric theme. In such cases failure to eliminate the effect of this theme can result in the generation of a variety of unusual, unexpected, and seemingly counterintuitive multivariate data-analysis results. This effect was first identified by Felix Klein who described certain aspects of this issue in a 1926 article with specific focus on the analysis of the logarithmic spirals of ammonite shells. However, this problem is much more general than Klein (1926) alluded to and can potentially affect, to a greater or lesser extent depending on the range of shape variation included in the sample, any dataset collected from any sample and represented by any set of metric variables. Fortunately, it is a simple matter to correct morphometric data for the effect of dominant geometric themes. This normalization has long been a part of the geometric approach to morphometric analysis. But it can and should be used in a wider variety of data-analysis contexts. The significance of, and discussion of solutions for, the dominant geometric theme effect are presented here primarily in the context of differential geometries of ammonite microconch and macroconch dimorphs.

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1. Introduction

Many ammonoid shells or phragmacones are coiled in close approximation to the geometry of the logarithmic spiral. This imposes a constraint on the results of ammonoid morphometric analyses based on measurements made on the shell in lateral aspect. One of the inescapable complications of an eigenanalysis of the covariance matrix calculated from such data is that this matrix will be virtually of unit rank as a consequence of the strict and predictable conformance to the form of the logarithmic spiral which constitutes a dominant geometric theme from which individual shells depart only slightly.

This mathematical issue was first recognized by the German mathematician Felix Klein (1926) in his posthumously published Vorlesungen über Höhere Geometrie (Lectures on Higher Geometry). Klein's conceptualization of geometry as the properties of a space that are invariant under a given group of transformations—which effectively achieved a synthesis between Euclidean and non-Euclidean geometry—had a profound influence on the development of mathematics and remains relevant to modern applied and theoretical geometers (including morphometricians, see also Klein, 1872).[1] In order to illustrate the mathematical principles of spiral curves Klein (1926) employed a study of the geometry of ammonite shells. One of the main features of his presentation was the growth profiles for microconch and macroconch ammonite morphs.

In ammonites, microconch and macroconch forms (also termed micromorphic and macromorphic) are forms whose morphologies are identical in the early phases of their ontogenetic development, but diverge in their later developmental stages (e.g., de Blainville, 1840; Waggen, 1869; Quenstedt, 1886–1887; Brinkmann, 1929; Arkell, 1952; Makowski, 1962; Palframan, 1966; Verma and Westermann, 1973; Parent and Zatoń, 2016). Typically one dimorph reaches a markedly larger size than the other despite the fact that both exhibit all morphological markers associated with sexual maturity. Often ammonite dimorphs have been described as separate species, especially in regions where their occurrence is scarce and/or preservation poor. When recognized as belonging to

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[1] Klein also discovered the "Klein Bottle" which is a one-sided, four-dimensional closed surface that can exist (but not be embedded) in three-dimensional space.

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the same species, the presence of these two morphs has long been regarded as an example of sexual dimorphism with the larger, or macroconch, being interpreted originally as the male (Callomon, 1963, 1969). However, following Saunders and Spinosa's (1978) demonstration of sexual dimorphism in modern *Nautilus*, in which the larger morph is the female, this original interpretative convention was reversed to denote equivalence between the macroconch and the feminine gender as the more likely condition across all cephalopods in which sexual dimorphism has been recognized.

While Klein's illustration of the problems associated with the eigenanalysis of unit-ranked, square matrices was grounded on a consideration of ammonite morphology, the forms of many aspects of many other biological species are also based on spiral geometries (e.g., a very large number of foraminiferan and mollusc shells, sunflower florets, fern shoots, ram's horns, vertebrate cochlea, spider webs, see Cook, 1914, Thompson, 1917) as are the characteristic forms of many physical structures (e.g., hurricanes, spiral galaxies, vortices in fluid media). Moreover, the data-analytic issues described by Klein (1926) are not confined only to morphologies that exhibit a spiral form. They are potentially present in any set or sample of forms in which there exists a dominant geometric theme from which individual expressions depart to only a modest extent, irrespective of cause.

2. Statement of the problem

Klein (1926, pp. 171–173) noted that, owing to the geometric constraints imposted by adherence to the logarithmic spiral, the rank order of eigenvalues (= latent roots, see Hammerling, 1970; Jöreskog et al., 1976; Davis, 2002) extracted from a covariance matrix of measurements that document aspects of the ammonite coiling pattern will be very close to unity (sensu Zurmühl, 1964), irrespective of the composition of the sample (e.g., samples composed of different species, different morphs). This principle can be demonstrated by examining the decomposition of covariance matrices constructed from a set of standard ammonite conch measurements (Fig. 1) taken from specimens of *Discoscaphites conradi* illustrated Landman and Waage (1993) from which macroconch and microconch morphologies can be recognized (Table 1).

For each dataset, variation along the first eigenvector overwhelms that of all of the remaining eigenvectors combined. As this first eigenvector contains all positive variable loadings its proper interpretation is that of an allometric size–shape variation index with the scatter of data points projected to positions along this axis predominantly reflecting variation in shell size. Since variation in the non-size aspects of morphological patterning is so small in this result, most morphometricians and biometers would not be comfortable rendering interpretations of any but the first eigenvector, in which case all aspects of size-free shape variation in these data would remain unassessed.

The fact that this result is quite general among biometric analyses of data collected from ammonites can be demonstrated by calculation of analogous results for another species, *Jeletzkytes spedeni*, illustrated in the Landman and Waage (1993) monograph (Table 2).

As noted above, the basis for this extreme loading of geometric variation onto the first eigenvector of the covariance matrix is usually understood to be the constraint imposed by the conformance of the growth series to the logarithmic spiral. However, in these examples it is clear that, in the absence of pronounced shape variation owing to the operation of this constraint, the predominant component of geometric variation exhibited by these data is size variation. In studying aspects of form variation it has long been regarded as being of the utmost importance to be able to consider the issues of size variation and shape variation separately, as distinct features of morphological variation. But will the a priori removal of size variation from these data be sufficient to correct the problem?

Unfortunately, there is a wealth of divergent opinion regarding how to correct linear distance data for size variation (see Gould,

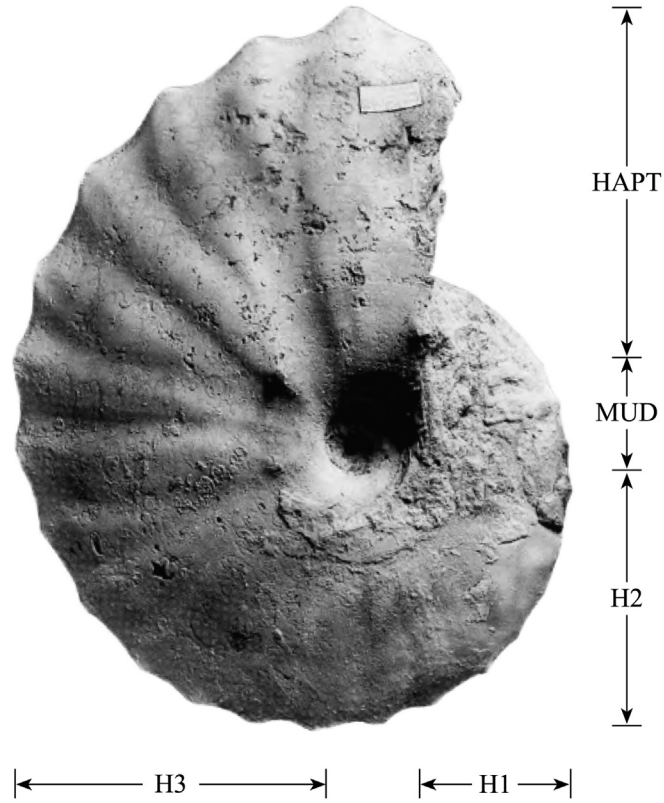

Fig. 1. Linear distance measurements used to quantify the morphology of the ammonite phragmacone in lateral view. HAPT: whorl height at aperture; H3: whorl height three quarters of the way around the ultimate whorl; H2: whorl height halfway around the ultimate whorl; H1: whorl height one quarter of the way around the ultimate whorl; MUD: maximum umbilical diameter. These measurements are standard dimensions that have been used to quantify the form distinctions between microconch and macroconch forms (e.g., Landman and Waage, 1993) and interspecific differences (e.g., Kennedy et al., 2009). The figured specimen is *Knemiceras dubertrei* Basse 1940, Oxford University Museum (OUM) KY92, from the Kazhdumi Fm., Tang-i-Shiraz, Hormozgan Province, Iran (illustrated originally in Kennedy et al., 2009).

Table 1
Eigen-decomposition of covariance matrices for the five standard ammonite biometric measurements shown in Fig. 1. Data collected from images of ammonite specimens included in Landman and Waage (1993).

Discoscaphities conradi (Morton)						
Macroconchs ($n = 11$)						
Eigenvector	1	2	3	4	5	$\sum$
Eigenvalue	6071.00	41.21	14.50	5.14	1.15	6133.00
Percent variation	98.99	0.67	0.24	0.08	0.02	100.00
Cum. percent variation	98.99	99.66	99.90	99.98	100.00	100.00
Microconchs ($n = 8$)						
Eigenvalue	2466.70	44.32	9.15	5.26	0.90	2526.33
Percent variation	97.64	1.75	0.36	0.21	0.04	100.00
Cum. percent variation	97.64	99.39	99.76	99.96	100.00	100.00
Combined macroconchs & microconchs ($n = 19$)						
Eigenvalue	9502.30	46.57	20.19	9.73	1.33	9580.12
Percent variation	99.19	0.49	0.21	0.10	0.01	100.00
Cum. percent variation	99.19	99.67	99.88	99.99	100.00	100.00

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