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Use of landmark and outline morphometrics to investigate thecal form variation in crushed gogiid echinoderms

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Abstract

Gogia is a primitive genus of pelmatozoan echinoderm the investigation of whose systematics, taxonomy, and palaeoecology has been invigorated recently by the recovery and description of articulated specimens and related genera of blastozoan species from Cambrian strata in Utah and China. To date investigation of gogiid systematics has been undertaken almost exclusively using qualitative methods to assess morphological variation owing, at least in part, to the crushed character of articulated fossils. This practice reflects the widespread belief among palaeontologists that quantitative approaches to morphological analysis can only be employed successfully on well-preserved specimens. Accordingly, no geometric morphometric analysis of gogiid morphology has been published to date. In order to investigate whether morphometric approaches to gogiid character analysis might be used to recover biological signals the thecae of 27 gogiid specimens collected from a single bedding plane were subjected to geometric analysis using landmarks, boundary outline equi-spaced semilandmarks, boundary outline sliding semilandmarks, and combined landmark + outline sampling protocols. Results indicate that, despite the crushed and deformed character of these specimens, robust and unquestionable biological signals can be extracted from the patterns of variation presented by these specimens by all the aforementioned methods. Based on these morphometric results it is concluded that (1) the sample exhibits several complex patterns and shape variation some of which may be inconsistent with the assumption that all specimens included in the sample should be assigned to the same species, (2) the primary pattern of thecal shape change appears to be highly correlated with an aspect of specimen size (thecal length) suggesting that various life-cycle stages are present within the sample, (3) assessments of right-left symmetry can be used to distinguish biological from post-mortem deformational aspects of shape variation, (4) the sliding semilandmark procedure failed to improve semilandmark correspondences across the sample and, indeed, appears to have degraded rather than improved the assessment of the biological shape variation, and (5) morphometric sampling strategies that combine the information recorded by landmarks and equi-spaced boundary outline semilandmarks appear to recover the greatest proportion of biologically interesting shape variation.

Keywords: Echinoderm; Morphology; Morphometrics; Shape; Systematics; Multivariate analysis

1. Introduction

The primitive eocrinoid genus *Gogia*, along with several related gogiid species, has recently become a subject of interest among echinoderm researchers owning to the discovery of several local faunas that contain articulated gogiid fossils (e.g., Huang et al., 1985; Zhao et al., 1994, 1999; Parsley et al., 2005; Parsley and Zhao, 2006; Lin et al., 2008a), including some putatively single-species populations from Utah in the western USA (Zamora et al., 2013). The existence of these well-preserved, articulated, gogiid faunas has provided an opportunity to re-examine the taxonomy of this group based on a variety of morphological criteria. To date, the only quantitative analyses of gogiid morphology appear to have been plate counts and thecal heights which were used by Zamora et al. (2013) to

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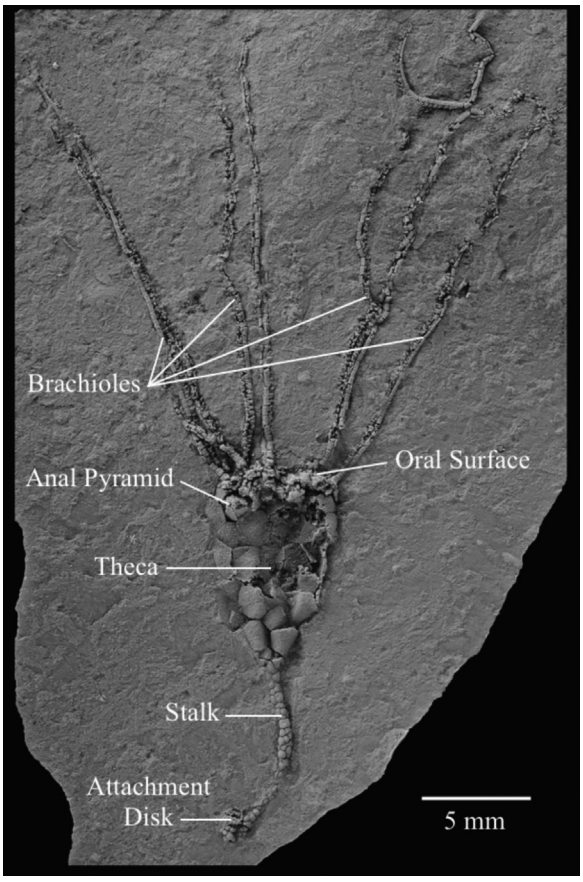

Fig. 1. Latex mould of typical articulated gogiid echinoderm from the Spence Shale Member of the Langston Formation (lower Middle Cambrian), Utah with major body parts labelled. Specimen G16-p93, currently residing in the collections of the US National Museum of Natural History, Washington, D.C.

infer aspects of gogiid ontogeny and population settling history respectively. In addition, Lin et al. (2008b) used stereom pore size, and trabecular thickness measurements to infer aspects of gogiid preservation. However, despite the existence of substantial deformation in some of the preserved bodies of articulated individuals, regularities in the gross forms of gogiid theca are susceptible to quantitative morphometric characterization. If morphometric approaches can be used to identify and document biologically meaningful discrepancies between the patterns of morphological variation in gogiid assemblages, this tool could be important in testing taxonomic hypotheses as well in providing a means to assess a wide range of developmental and life-history parameters for this group. Accordingly, the primary goal of this investigation was to explore the utility of different morphometric data-collection and data-analysis strategies that might be employed in the investigation of gogiid systematics and paleobiology.

Fig. 1 illustrates the primary morphological features of the gogiid body plan. As with all pelmatozoans, the gogiid body was covered completely by a series of 50–100 interlocking calcite thecal plates whose sizes and shapes differ depending on their function and ancestry, along with a cylindrical stalk covered by smaller plates that terminated distally with an attachment organ. Thecal plates are large and polygonal, forming a quasi-rigid cup within which the body viscera was set. Stalk plates were also polygonal though much smaller and more variably shaped than the thecal plates. By inference the gogiid stalk was also a semi-rigid structure, strong enough to support the thecae and brachioles, but flexible enough to allow some degree of movement in response to prevailing currents. Finally the terminal holdfast was covered by plates smaller in size and more variable in shape than the stalk plates. These likely served as a protective covering for the attachment organ that allowed it to conform to the shape of the attachment site as the body grew and more attachment area was needed to hold the stalked body fixed and upright.

The most complicated — and so least well-preserved — part of the gogiid body is the oral surface, which contains a set of smaller thecal plates bearing sutural pores arrayed around a central mouth from which five radially oriented ambulacra emanate. Each oral ambulacrum terminated in a brachiole, each of which was formed by a small biserial set of plates bearing a food groove on the oral side protected by small cover plates. Articulations between these plates lend this structure the flexibility and wide range of movement necessary for their primary food-gathering function.

The symmetry of this oral surface is not perfectly pentaradiate because (1) the area containing the anal pyramid is slightly wider than the other interray areas and (2) ambulacra A, C and D appear to develop earlier in ontogeny than ambulacra B and E (personal comm., James Sprinkle, 2015). While this slight asymmetry is best expressed externally in the geometry of the oral surface, it reflects a deeper asymmetry in the soft-part anatomy of the gogiid body. Nevertheless, the primary structural elements of the gogiid theca are formed by the plates forming the bulk of the thecae and the symmetry of this structure overall is not far from the pentaradiate condition.

Owing to the flexibility of the brachioles and stalk, these features are oriented variously in articulated fossil gogiid specimens, thus rendering their morphometric characterization difficult. Similarly, the holdfast is small relative to the rest of the body and compromised as an important taxonomic character by its need to conform — to a greater or lesser extent — to the form of the substrate. It is also often the case that the holdfast is either missing or partially preserved in many gogiid specimens, probably having been separated from the stalk via breakage by whatever event led to the original dislodgement and rapid burial of the body (see Lin et al., 2008a). While the plates that comprise these features of the fossil may themselves be subject to morphometric analysis, the complex variability of their orientations across a sample of gogiid fossils, which derive, in turn, from their functional need to retain some measure of flexibility, makes them unsuitable targets for morphometric analysis.

However, the cup-like theca is far more rigid than any other part of the body, retaining most aspects of its form even when its constituent plates exhibit a high degree of disarticulation due to decay and/or post-mortem crushing from the weight of overlying sediment. While the fine details of the thecal outline may have been rendered more irregular then they would have been in life by these taphonomic processes — especially in